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Science and imagination

By those unfamiliar with it, science is commonly looked upon as a strictly objective and unimaginative pursuit in which the personality of the individual research worker is not reflected. Progress, it seems, is the result of faithfully following an established procedure, each new step forward being the logical and considered sequel to the one which preceded it. Casual perusal of the journals in which the results of new research are reported seems to confirm this. There, all follows a clear pattern: new facts are discovered by experiment or observation and then fitted neatly into a framework of unifying explanation. Yet how different, in most instances, is the reality. How often does the inspired guess—the product of some scientific instinct, partly inherent and partly bred of experience—reveal the truth long before it could have been uncovered by conventional methods. Claude Bernard was firmly of the opinion that ideas are of far greater importance than facts: '*on donne généralement le nom de "découverte" à la connaissance d'un fait nouveau; mais je pense que c'est l'idée qui se rattache au fait découvert qui constitue en réalité la découverte.*' Such ideas, of course, are not always right—and then we hear no more of them—but when they are they save a vast amount of time and effort, for only one possibility, and not many, needs to be confirmed.

Thus imagination, far from being unnecessary in science, is a most useful asset, and exceptional fertility of imagination is a quality which distinguishes the truly great scientist from his fellows. The history of science offers innumerable examples to support this thesis. Kekulé's imaginative conception of the quadrivalency of carbon and the union of carbon atoms, and his sudden vision of the benzene molecule as a snake seizing its own tail, come immediately to mind. The explanation of aberration came to James Bradley as he was sailing on the Thames. Today, when the pace of scientific progress has so greatly accelerated, too little time is given to exercising the imagination. There is much merit in Kekulé's advice: '*Lernen wir träumen, dann finden wir vielleicht die Wahrheit.*' Problems in mathematics, too, commonly resolve themselves more readily by intuition than by the logical application of established rules. Poincaré has described how a major discovery in the theory of fuchsian groups and functions, upon which he had long been pondering, came to him as he boarded an omnibus at Coutances; again, walking by the sea, he suddenly realised a property of indefinite ternary quadratic forms which had not hitherto been apparent. William Whiston has recorded that in mathematics Newton 'could sometimes see almost by intuition, even without Demonstration. . . . And when he did but propose conjectures in Natural Philosophy, he almost always knew them to be true at the same Time. . . .' Sir Charles Parsons related that his mathematical work was done by obscure mental processes which even he himself did not understand. Having reached the goal, it is sometimes easy to see how it could have been achieved by going from one firm stepping-stone to another. Sometimes, however, it is years before the intermediate steps are clear, but in the meantime the result may be put to use.

In science the means for progress often exist long before they are utilized; the facts necessary for the formulation of some important generalization may be common knowledge long before their collective significance is apparent. Here again it is the imaginative mind, rather than the logical, which perceives new significance and an underlying pattern in something known to all. Thus the fact that friction generates heat has been known from ancient times, for it is a primitive method of making fire, but it was Rumford who first clearly saw and formulated the significance of the relationship between work and heat. Anomalies in the eclipses of Jupiter's moons were well known before Rømer advanced the correct explanation, that light has a finite velocity. Giovanni Cassini, himself no mean thinker, had for a short time toyed with this hypothesis, but had discarded it, and he strongly opposed Rømer's theory when it was first enunciated. Such failure to perceive the force of new theories is by no means rare in the history of science. Thus Priestley remained a convinced phlogistonist until the day of his death, although his own experiments with red calx of mercury played no small part in leading Lavoisier to a true understanding of the nature of combustion. Such lack of understanding is particularly surprising, for Priestley himself condemned those unreceptive of new ideas: 'we may take a maxim so strongly for granted that the plainest evidence of sense will not entirely change, and often hardly modify, our persuasions.' What Priestley is condemning is, in effect, lack of imagination.

In the design of experiments imagination may play as vital a role as it does in the interpretation

of results. '*Toute l'initiative expérimentale est dans l'idée, car c'est elle qui provoque l'expérience,*' wrote Bernard. The good experimentalist is he who, free from preconceived ideas, sees quickly and clearly what must be demonstrated and how it may most simply be done. Others might eventually reach the same conclusion, but with less elegance and more labour.

While the general progress of science depends upon the development of the original ideas of a comparatively few men, the work of development, too, demands considerable powers of imagination. The application of new conceptions, whether for the purposes of further research or for practical ends, almost invariably poses a variety of difficult problems. At all levels of science, both pure and applied, imagination plays an important role.

While a fertile imagination is thus not merely useful but essential, it is a characteristic which must not become dominant. Science itself is objective and not subjective, and while speculation may rightly form both prologue and epilogue to experiment, it can have no part in the latter, where objectivity is essential. Results which fail to fit in with preconceived theories must not be ignored unless some reason for the deviation is clear; as in the case of Jupiter's moons, it is often the discrepant result which is the most significant. Uninhibited speculation has no place in science, and it is very right that all new theories not fully substantiated by facts should be treated with reserve. While one might cite many examples of undeserved scepticism having delayed general acceptance of important theories, it must not be forgotten that the same scepticism has ensured the early death of innumerable ideas which were in fact worthless.

It is perhaps this ceaselessly questioning attitude of mind, coupled with the need for strict objectivity in the laboratory, which has led to the present popular conception of the scientist as an unimaginative being interested only in material matters. In a world growing daily more dependent upon the fruits of scientific research and their application, such conceptions, like all others which seem to set scientists apart from the rest of the community, are dangerous. Such misunderstanding breeds suspicion, and scientists, far from being looked upon as potential benefactors, are feared as possible instruments of suffering and destruction; as a result there is prejudice against their participating in the wider fields of human affairs. Clearly they must, as scientists, participate in such affairs only in so far as their special technical knowledge may be helpful; it cannot be argued that scientific knowledge alone is a qualification entitling its possessor to influence in fields where such imponderable factors as human emotions and desires play major parts. Yet imagination is among the most important qualities necessary for solving the grievous problems which beset the world today, and recognition of the fact that it is one which scientists may possess in considerable degree would surely encourage their useful employment in wider fields. But such a move demands support from both sides. The scientist must realize that unless he is speaking of purely technical matters he is entitled to a hearing only in respect of his other qualities. Equally, those responsible for the formulation of policy must more generally realize that the ability of scientists is not necessarily confined to purely scientific matters.

At the moment, unfortunately, the gap can be bridged only from the side of science. While many men trained in the discipline of science have subsequently proved their ability to assist in the formulation of policy and to undertake administration at the highest levels, the opposite transition is virtually unknown. For this state of affairs there is a good and obvious explanation: for social and economic reasons, specialized training, whether in science or anything else, is possible virtually only in early life. With the best will in the world, older men established in positions which oblige them to make major decisions relating to scientific matters cannot enter on a course of scientific study detailed enough to be useful. But the young scientist who has just completed his studies has a wide choice of useful careers in front of him if he and his prospective employers are willing to make his scientific training not his sole means of livelihood but a means of bridging the gap between science and the vast range of other affairs which it now influences. With a sufficiently large number of trained scientists thus placed in administrative posts the tide might eventually flow in both directions. Men trained in science and having experience of the practical problems of everyday affairs might eventually find their way back to the scientific world, with advantage to both.

Photosynthesis

C. P. WHITTINGHAM

The importance of increasing the world's food supply to keep pace with its rapidly increasing population, and of increasing its fuel supply to permit the vast industrial expansion upon which our modern standard of life depends, needs no emphasis. In both connections study of photosynthesis is of fundamental importance. Not only is it the process by which green plants produce our principal foodstuffs but it is a process by which solar energy is converted into chemical energy potentially useful for industrial purposes. Analysis of the successive reaction steps indicates that photosynthesis is probably not a biochemically unique process.

Early investigators of photosynthesis showed that a green plant exposed to light apparently reversed the ordinary process of respiration common to all living organisms—it took up carbon dioxide and water and produced organic compounds and oxygen:

$$CO_2 + H_2O \underset{\text{respiration (dark)}}{\overset{\text{photosynthesis (light)}}{\rightleftharpoons}} \text{Organic C compounds} + \tfrac{1}{2}O_2$$

In the leaves of some dicotyledons the organic compound can be detected as starch; in other leaves sugar accumulates; in some algae fats are formed. In green wheat leaves, protein formation is accelerated by illumination in the presence of carbon dioxide. The production of these diverse foodstuffs can be understood if we assume the initial product of photosynthesis to be a sugar occupying a central position in the metabolic pool, for example a triose. Fats, amino acids and proteins, sugars and carbohydrates, may be formed from such a triose by known enzyme mechanisms common to all living organisms.

The overall process of photosynthesis can now be split up into several reaction steps. First, the absorption of radiant energy by the pigment system; second, the stabilization of this energy in some chemical form; and, finally, the transfer of this energy for the reduction of carbon dioxide.

THE PIGMENT SYSTEM

The pigment system concerned with photosynthesis in the green leaf is localized in ellipsoidal bodies within the cell, the chloroplasts. Within the chloroplasts the pigments are concentrated in the grana in disk-like regions; these are stacked like piles of coins, but are separated from each other by areas relatively free of pigment. In algae there is a greater diversity of chloroplast shape, but the basic structure is probably analogous. It is assumed that within the differentiated layers of the chloroplast the individual pigments are arranged in an organized manner. These pigments are of two types: blue-green chlorophyll *a* and yellow-green chlorophyll *b*, and the carotenoids, yellow xanthophylls and orange carotenes. When other pigments, such as the red and purple anthocyanins, are present, they are dissolved in the cell sap and play no direct part in photosynthesis. The algae show a greater diversity of carotenoid pigments, and the blue-green and red algae contain, in addition, representatives of a further class of compounds, the phycobilins. The phycobilins are soluble in water; the chlorophylls contain both hydrophilic and hydrophobic groups and are soluble in organic solvents; the carotenoids are soluble in fats. This diversity of properties indicates at least a two-phase system in the pigment centres in the chloroplast.

Within the grana the pigments are highly concentrated, perhaps as high as 0·1 molar. However, since the absorption spectrum of chlorophyll in the plant is simply related to that of chlorophyll in solution, excitation may still be regarded as an act of absorption by an individual molecule. There is evidence that in an organized structure of high pigment concentration, such as the grana, any individual excited molecule may transfer its energy to an adjacent molecule of the same or a different kind. The fluorescence yield of chlorophyll in the plant is about one-tenth or one-hundredth of that of chlorophyll in solution, indicating that the life of the excited molecule is such that about one hundred transfers is the maximum possible during the excitation period. Two lines of evidence indicate that such transfer of energy between molecules does occur.

If allowance is made for a shift in the wavelength for maximum absorption and for some broadening of absorption bands *in vivo*, the absorption and fluorescence spectra of a green cell can be related

with a reasonable degree of certainty to the spectra of the pigments which can be isolated from it. When, however, the cell absorbs light of one wavelength, which *in vitro* would result only in fluorescence characteristic of one pigment, it is found that the light emitted contains fluorescence characteristic of a second pigment present. For example, in a suspension of diatoms illuminated with light of a wavelength which is predominantly absorbed by the carotenoid fucoxanthol, the fluorescence is similar in quality and intensity to that emitted when the exciting light is absorbed only by chlorophyll. In the cell, energy must therefore have been transferred from the fucoxanthol, which absorbed the light, to chlorophyll. Similarly, transfer of energy has been demonstrated from chlorophyll *b* to chlorophyll *a* in green algae, and from the phycobilins to chlorophyll in the red and blue-green algae.

Prior to studies of the sensitization of the fluorescence of one pigment consequent upon absorption by a second pigment, it had been shown that the photosynthetic efficiency of light absorbed by carotenoids in the green alga *Chlorella* was about half that of light absorbed by chlorophyll; light absorbed by fucoxanthol in diatoms was about as efficient as that absorbed by chlorophyll; and that of light absorbed by phycobilins in blue-green algae about as efficient as absorption by chlorophyll. It was found that in the red algae the efficiency of light absorbed by phycoerythrin was greater than that for light absorbed by chlorophyll; this was later found to be true also for the sensitization of fluorescence of chlorophyll. This has been attributed to the existence in the red algae of a form of chlorophyll, chlorophyll *d*, which is inactive with respect to both fluorescence and photosynthesis, but to which energy may be transferred; it is suggested that phycocyanin and phycoerythrin transfer excitation energy preferentially to chlorophyll *a*. The measurements indicate that transfer of energy must occur with high efficiency within the plant.

The mechanism of energy transfer is assumed to be that of inductive resonance. The excited molecule is associated with an electric field with vibration frequencies determined by that of the light emitted; if a neighbouring molecule is able to absorb energy of these frequencies, it may itself be excited. Thus, the necessary condition for energy-transfer is that the fluorescence spectrum of the excited molecule overlaps the absorption spectrum of the receiver. Using Förster's equation, L. N. M. Duysens [1] has shown that, with the concentrations of chlorophyll *a* and *b* found in *Chlorella*, we should expect almost complete transfer of excitation energy from *b* to *a*. This would result effectively in the absence of any fluorescence characteristic of chlorophyll *b*, and this is indeed so (figure 1). Similarly, it can be shown that the almost complete transfer of energy from phycoerythrin and phycocyanin to chlorophyll is not inconsistent with the theory of transfer by induced resonance.

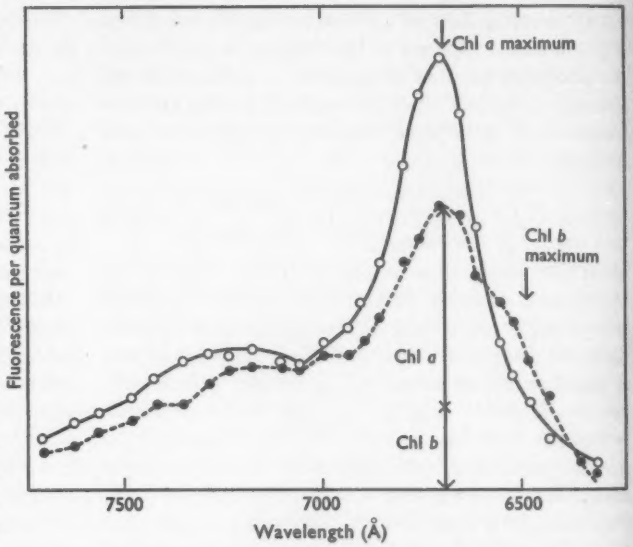
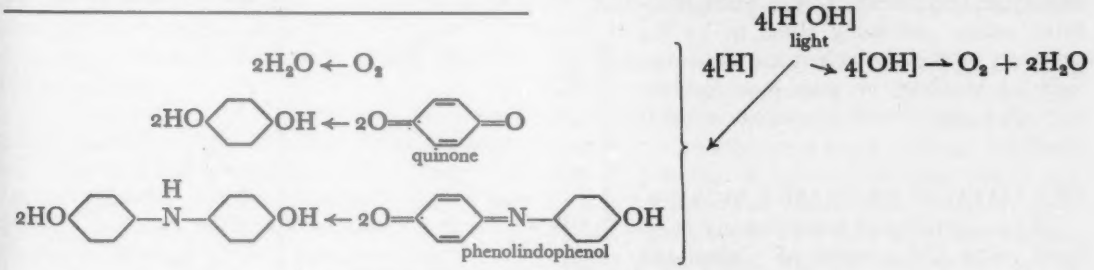


FIGURE 1 – *Energy transfer between pigments in solution. Fluorescence spectra for chlorophylls in ether solution when irradiated with a wavelength of* 4290 *Å* (70 *per cent absorption due to chlorophyll* a) *and with* 4530 *Å* (95 *per cent absorption by chlorophyll* b). *The vertical line at* 6700 *Å indicates that in the second case a large portion of the fluorescent light is characteristic of chlorophyll* a, *whereas chlorophyll* b *was the pigment excited: partial transfer of energy from chlorophyll* b *to chlorophyll* a *has taken place. In the living cell the pigments are more concentrated and transfer is practically complete.* o = *exciting light* 4290 *Å.* • = *exciting light* 4530 *Å.* (*From L. N. M. Duysens, Ph.D. thesis, Utrecht,* 1952.)

The pigment having an absorption maximum at the longest wavelength, chlorophyll *a*, is found in all plants except the bacteria; in the latter, bacteriochlorophyll plays a similar role. Thus all the pigments of the chloroplasts can ultimately contribute energy to chlorophyll *a*. The presence of a diversity of pigments merely extends the range of absorbed wavelengths effective in photosynthesis; this is a feature of some ecological significance in certain habitats.

ABSOLUTE QUANTUM EFFICIENCY

In contrast with the general agreement as to the relative efficiency of light of different wavelengths, there is not yet agreement about the absolute value for the maximum efficiency of photosynthesis. Values for the efficiency of conversion of free energy vary from 30 per cent up to 90 or even 100 per cent, i.e. a quantum yield in red light (6600 Å) of between 0·1 and 0·3 molecules O_2 per quantum. The majority of workers agree that the highest values are not firmly established; on the other hand, O. Warburg and his collaborators reaffirm their observations of high efficiency under a wide range of conditions [2]. Various suggestions have been put forward to explain this difference of opinion. The most probable is that many workers have used relatively brief light periods in order to make the correction for dark metabolism as precise as possible. During such periods, side reactions may play a role comparable with that of photosynthesis proper, vitiating the free energy calculation. Also, recent evidence has shown that *Chlorella* exhibits two morphological forms which differ in chlorophyll content and photosynthetic efficiency [3]; considerable variation in physiological properties also exists without change in gross morphology. Nevertheless, even accepting the lowest estimate, the efficiency of the overall process of photosynthesis in the living plant compares favourably with that of any other photochemical mechanism for the conversion of light energy.



General equation (A = acceptor):

$$4H_2O + 2A \xrightarrow{\text{light}} 2H_2O + O_2 + 2AH_2$$

THE PRIMARY CHEMICAL STEP

The classical biochemical approach to the study of metabolism is to break up the cellular structure in an attempt to isolate individual reaction steps; the reaction system can then be ultimately analysed into pure chemical constituents. Using photosynthetic organisms, the only advance which has been made in this direction is the study of reactions catalysed by chloroplasts isolated from the cell. In the late nineteenth and early twentieth century it was thought that isolated chloroplasts were still able to carry on photosynthesis, though at a much reduced rate. In 1937 R. Hill [4] showed that isolated chloroplasts had no measurable affinity for carbon dioxide in the light; if, however, they were supplied with more easily reduced substances, such as ferric salts, instead of carbon dioxide, the ferric ion was reduced and oxygen was set free. It has now been shown that a variety of substances can be reduced—for example quinone, ferricyanide, and some dyestuffs—with the evolution of the equivalent amount of oxygen. This type of reaction is called the Hill reaction or chloroplast reaction. Under some conditions oxygen may itself act as a hydrogen acceptor, forming hydrogen peroxide; this breaks down to oxygen and water, resulting in no overall reaction. If the chloroplast reaction takes place in the presence of water labelled with O^{18}, it is found that all the oxygen evolved originates from the water, and none from the chloroplast material or from the substance reduced. The chloroplasts act only as a photocatalyst; they need not be complete, since fragments will suffice. Thus a general equation can be written representing the chloroplast reaction as a 'splitting' of water; water and the radicals are not postulated to exist in a free state but rather in the form of a complex (indicated in the equation by a square bracket), probably with enzymic protein.

If the direct reduction of certain biological substances, such as cytochrome or coenzyme I or II, is attempted using illuminated chloroplasts, little effect is observed, probably because of rapid reoxidation of any of the reduced form produced. But by coupling the chloroplast reaction with other systems in which the reduced form is rapidly

consumed, and by maintaining a low concentration of oxygen, indirect evidence for reduction is obtained. By using the reaction systems shown in the following equations, W. Vishniac and S. Ochoa and others [5] demonstrated the reduction of both coenzyme I and coenzyme II in the chloroplast reaction.

$$H_2O + CoII \xrightarrow[\text{chloroplast}]{\text{light}} CoIIH_2 + \tfrac{1}{2}O_2$$

$$\text{Pyruvate} + CO_2 + CoIIH_2 \xrightarrow[\text{enzyme}]{\text{malic}} \text{Malate} + CoII$$

$$\text{Pyruvate} + CO_2 + H_2O \longrightarrow \text{Malate} + \tfrac{1}{2}O_2$$

$$H_2O + CoI \xrightarrow[\text{chloroplast}]{\text{light}} CoIH_2 + \tfrac{1}{2}O_2$$

$$\text{Pyruvate} + CO_2 + CoIH_2 \xrightarrow[\text{dehydrogenase}]{\text{lactic}} \text{Lactate} + CoI$$

$$\text{Pyruvate} + CO_2 + H_2O \longrightarrow \text{Lactate} + \tfrac{1}{2}O_2$$

If mitochondrial preparations from plant or animal tissue are added to illuminated chloroplasts, oxidative phosphorylation results. It is assumed that this represents a coenzyme coupled system, reduction of the coenzyme by the chloroplast system being followed by reoxidation of the reduced coenzyme via mitochondria, resulting in phosphorylation.

Thus the chloroplast reaction system represents, upon illumination, a potential supply of hydrogen in the form of reduced coenzyme and thence also of phosphorylated esters. Assuming these to be the products of the photochemical or water-splitting reaction, we may next consider how they are related to carbon dioxide fixation.

THE FIXATION OF CARBON DIOXIDE

The availability of the relatively long-lived tracer C^{14} enabled M. Calvin and his colleagues to advance earlier researches which had been limited to the use of the short-lived tracer C^{11} [6]. The earlier work showed that if $C^{11}O_2$ was supplied in the dark to a green plant, activity appeared largely in carboxyl groups; under illumination, compounds largely free of carboxyl groups were labelled. In later experiments with $C^{14}O_2$, the analysis of products was made easier by the advent of new paper-chromatographic methods. This provided an analytical technique sufficiently delicate for the exploitation of the great sensitivity of the tracer method. The technique has been applied mainly to *Chlorella* and other algae, but some observations have been made with higher plants. After exposure to $C^{14}O_2$, the plant was rapidly killed in boiling alcohol and extracted successively in 80 per cent and 30 per cent alcohol, and the combined extracts were concentrated in vacuo. Two-dimensional paper chromatograms were then run, and active spots were identified by autoradiographs. After periods of illumination lasting several minutes, a large variety of carbon compounds, including sugars, fats, and proteins, showed radioactivity. As the period of illumination was shortened, the number of labelled compounds diminished, and at first it was argued that, in the limit, the compound in which activity first appeared must be the first product of photosynthesis. Later, curves were obtained in which the activities of individual compounds (as a fraction of the total carbon fixed) were plotted against time, and the curves were extrapolated to zero time (figure 2). Such curves clearly indicate that phosphoglyceric acid (PGA) is the first detectable compound to be labelled, and amounts to three-quarters of the total carbon fixed after two seconds illumination. Other compounds labelled at the outset include malic acid, free glyceric acid,

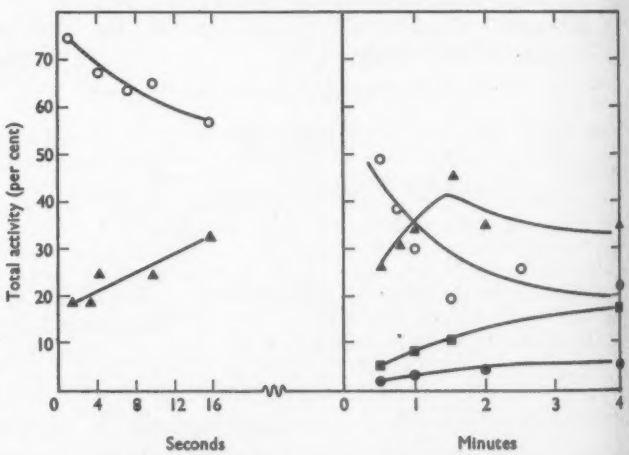


FIGURE 2 – *The percentage radioactivity incorporated in different compounds as a function of time during photosynthesis in* Scenedesmus *in presence of* $C^{14}O_2$. o = *phosphoglyceric acid.* ▲ = *sugar phosphates.* ■ = *malic and aspartic acids.* ● = *alanine.* (*After Calvin, M., Bassham, J. A., Benson, A. A., Lynch, V. H., Ouellet, C., Schou, L., Stepka, W., and Tolbert, N. E., in* Symp. Soc. exp. Biol., 5, 284, 1951, *and Bassham, J. A., Benson, A. A., Kay, L. D., Harris, A. Z., Wilson, A. T., and Calvin, M., in* J. Amer. Chem. Soc., 76, 1760, 1954.)

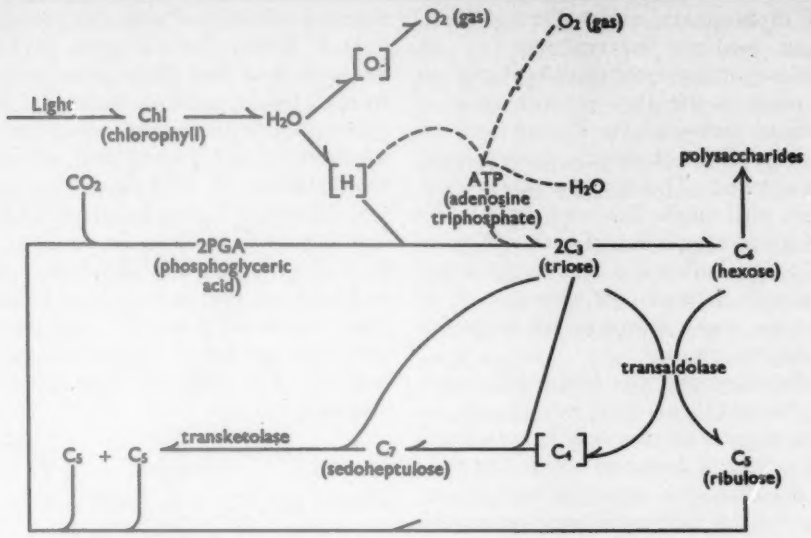


FIGURE 3 – *The path of carbon in photosynthesis as proposed by Calvin and colleagues.*

phospho-enolpyruvic acid, and a small amount of sugar phosphate esters. When the time of illumination is lengthened, the relative activity of PGA falls rapidly; that of some other compounds, e.g. phospho-enolpyruvic acid, increases to a maximum and then subsequently falls; a third group, represented by sucrose and alanine, shows a continuous increase. It is argued that the latter group represents final products, the second intermediates, and the first initial products.

For short periods of illumination, the radioactivity in PGA is confined to the carboxyl group, suggesting that it is formed by addition of carbon dioxide to some carbon precursor. Later the molecule becomes uniformly labelled, indicating the regeneration of further precursor containing the carbon dioxide already incorporated. An indication of the nature of this precursor has come from a study of the labelling sequence in the other compounds that are labelled early in illumination. Hexose is initially labelled in carbon atoms 3 and 4, and later in all six; thus the hexose probably arises from PGA. Sedoheptulose phosphate is at first labelled in carbon atoms, 3, 4, and 5 and ribulose phosphate in carbon atoms 3 and, to a lesser extent, 4 and 5. Thus the ribulose cannot arise directly from hexose, but must come from the 7-carbon compound. The following equations indicate the mechanism proposed by Calvin, which is summarized in figure 3.

$$3C_5 + 3C^*O_2 \rightarrow 6PGA\ (C_3C_2C_1^*) \quad \ldots\ldots(1)$$

$$PGA \rightarrow \text{triose phosphate}\ (C_3C_2C^*) \rightarrow \text{hexose}^1\ (C_3C_2C_1^*C_1^*C_2C_3) \quad \ldots(2)$$

$$\text{hexose} + 2\ \text{triose} \rightarrow \text{pentose} + \text{sedoheptulose} \quad \ldots(3)$$

$$C_1C_2C_3^*C_4^*C_5C_6 \quad C_3C_2C_1^* \quad C_3^*C_2C_1C_5C_6 \quad C_1C_2C_3^*C_4^*C_1^*C_2C_3$$

$$\text{sedoheptulose} + \text{triose} \rightarrow 2\ \text{pentose} \quad \ldots\ldots(4)$$

$$C_1C_2C_3^*C_4^*C_5^*C_6C_7 \quad C_3C_2C_1^* \quad C_1C_2C_3^*C_4^*C_5^* \quad C_3C_2C_1^*C_6C_7$$

Kinetic evidence for such a mechanism was obtained from a suspension of *Chlorella* by rapidly reducing the concentration of carbon dioxide during photosynthesis; a rapid increase in labelling of 5-carbon compound resulted, while the 3-carbon compound diminished. Further, after illumination ceased, there was a fall in 5-carbon compound labelling, together with an increase in that of the 3-carbon compound. These experiments clearly show an interrelation between the 3- and 5-carbon compounds. The enzymes which catalyse reactions (3) and (4), transaldolase and transketolase respectively, have been obtained from spinach leaves. Calvin and colleagues [7] have prepared sonic extracts from *Chlorella* which in the dark will fix carbon dioxide when supplied

[1] The number of any carbon atom in the product is that which it had in the reactant. Thus in hexose, atoms 1, 2, and 3 arose from one molecule of triose and 4, 5, and 6 from a second: hence it is written $C_3C_2C_1C_1C_2C_3$.

with ribulose diphosphate, and will form PGA. This represents evidence for reaction (1). E. Racker [8] has shown that homogenates of spinach leaves can catalyse in the dark the conversion of carbon dioxide to carbohydrate if adenosine triphosphate (ATP), ribose phosphate, and reduced coenzyme are supplied. Thus a reasonable mechanism consistent with all the known facts may be developed for the incorporation of carbon dioxide into sugars. It follows that the function of light-energy is to supply reduced compounds, such as reduced coenzyme, and a means for phosphorylation of sugar derivatives.

The possibility remains that important intermediates in photosynthesis may not appear in tracer studies if they are present only in very small amounts or if activity is localized within the cell. There is also the difficulty, universal with tracer methods in this field, of distinguishing components labelled by a pathway unrelated to photosynthesis but nevertheless affected by light. In *Chlorella* a large metabolic pool of carbon compounds is filled under dark aerobic conditions; upon illumination a 'burst' of evolution of carbon dioxide takes place which is probably related to the 'dark' pool [9]. The substances concerned have not yet been chemically identified, but it appears very probable that they are different from those postulated by Calvin in his present scheme. We might then distinguish a light-cycle of 3-, 5-, and 7-carbon compounds from, for example, the well known Krebs dark cycle of 2-, 4-, and 6-carbon compounds. The present position offers great encouragement for a systematic study of enzyme systems concerned with carbon fixation in the green plant.

THE ROLE OF CHEMOSYNTHESIS IN PHOTOSYNTHESIS

The mechanism of production of the phosphate esters which are probably concerned in the photosynthetic fixation of carbon dioxide is not yet known. There is evidence that in *Chlorella* the amount of ATP increases during illumination [10]. Comparative biochemistry suggests that ATP might arise from an oxidative process, the substrate for which could be part of the reduced product formed in the chloroplast reaction. As mentioned previously, additions of mitochondrial preparations to illuminated chloroplasts results in the formation of ATP. A cytochrome peculiar to green tissues, cytochrome *f*, has been obtained in relatively pure form; it is possible that this may play a role in photosynthesis in the reoxidation of reduced substances with the generation of ATP.

D. I. Arnon and colleagues [11] have recently demonstrated that chloroplast preparations from spinach leaves, carefully isolated so that the whole chloroplast is preserved (most previous workers used fragmented chloroplasts), are able to catalyse the formation of ATP from inorganic phosphate and adenosine monophosphate (AMP) at a rate four to twenty times greater in light than in dark. Such preparations also fix labelled carbon dioxide and have resulted in the recent claim that chloroplasts separated from the cytoplasm are able to complete the whole photosynthetic reaction sequence. The reaction steps shown below were proposed:

$$H_2O \xrightarrow[\text{chloroplast}]{\text{light}} 2e + 2H^+ + O \quad \ldots.(5)$$

$$AMP + 2H_3PO_4 + 2e + 2H^+ + O \rightarrow ATP + H_2O \quad \ldots\ldots\ldots\ldots(6)$$

$$AMP + 2PO_4 \rightarrow ATP$$

Work is continuing to identify the compounds in which the tracer carbon is incorporated. An attempt is also being made to separate, if possible, the enzymic system concerned with phosphorylation from that concerned with carbon reduction.

The mechanism suggests two possibilities. The first is that oxygen is liberated in reaction (5) and reconsumed in reaction (6). In this case, reaction (6) would be analogous to the overall reaction in chemosynthetic organisms, i.e. organisms which obtain the whole of their energy for carbon dioxide reduction from the oxidation of some chemical substance, such as H_2S, present in their environment. Warburg and his collaborators favour such a chemosynthetic mechanism in photosynthesis in *Chlorella*, because they find that brief alternate periods of light and dark result in changes in the rate of oxygen production and consumption which might be interpreted as being due to the gradual development in light of an oxygen-consuming reaction followed by a general decay in the dark. A second alternative appears more probable. Oxygen, as such, need not itself be utilized for the formation of ATP, but rather the oxidized radical formed from the 'splitting' of water. In support of this view, A. H. Brown [12] has shown, using isotopes of oxygen, that the consumption of oxygen from the gas phase by *Chlorella* is unchanged as a result of illumination (figure 4). Arnon has also recently shown that phosphorylation during illumination by whole chloroplast preparations proceeds more rapidly under anaerobic

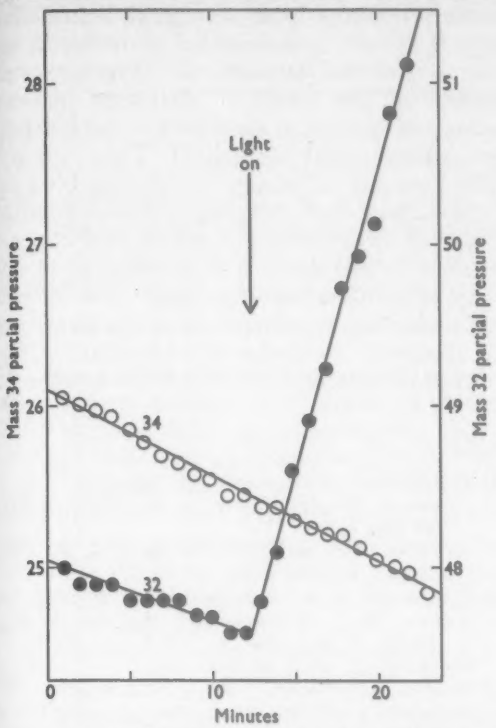


FIGURE 4 – *Differentiation between the simultaneous processes of oxygen uptake due to respiration and of oxygen production due to photosynthesis in light, using oxygen isotopes. O^{34} was present in the gas phase, and its consumption is proportional to the rate of respiration. O^{32} was present in the water also and is consumed in the dark, but consumed and produced in the light due to 'water splitting' in photosynthesis. Calculation shows that the rate of oxygen consumption is unchanged by illumination. (From van Norman, R. W., and Brown, A. H.,* Plant Physiol., 27, 691, 1952.)

than under aerobic conditions. This implies not only that oxygen is unnecessary, but that it is, in fact, inhibitory; this is possibly due to the re-oxidation of reduced intermediates by an alternative pathway. Frenkel [11] has shown the same to be true for preparations from the photosynthetic bacterium *Rhodospirillum rubrum*.

Information about the ratio of the oxidized to the reduced forms of certain hydrogen carriers *in vivo* can be obtained if the two forms differ in their absorption spectrum. Duysens [13] examined the change in the absorption spectrum brought about by illumination of a *Chlorella* suspension, and found a change in absorption in the visible spectrum, which could be interpreted as an increased ratio of oxidized to reduced cytochrome *f*, together with changes in the ultra-violet spectrum, which could be due to an increase in reduced coenzyme. The data are such that the interpretation is equivocal; it is, however, consistent with our general concept of the mechanism of photosynthesis. Similar effects have been observed by H. T. Witt [13], who suggests, however, that the changes in absorption by *Chlorella* consequent on illumination may be related to the excited states of chlorophyll.

The time courses of oxygen production and carbon dioxide consumption during the first minutes of illumination show a close relationship; it is somewhat closer than might be expected *a priori* if water-splitting and carbon reduction represent two independent reaction systems. It appears possible that in the living cell there is an obligatory rate-coupling between the two systems, due to the need for ATP in the reduction cycle and its generation from the oxidized radical produced from water.

PROBLEMS FOR THE FUTURE

The mechanism discussed is not to be considered as rigorously established; rather it begins to show how photosynthesis is taking its place in the general field of biochemistry. Photosynthesis no longer appears as a process unique to green plants: it appears to proceed in a manner which the modern biochemist might have predicted. But further observations are needed. Perhaps it is that one not only looks for an interpretation consistent with what is already known, largely from studies of dark metabolism, but ignores unidentifiable spots on the chromatograms which could hold the secret of any unique characteristic of photosynthesis.

It is certainly true that where comparative biochemistry ceases to help, in the borderland between the physics and the chemistry of photosynthesis, we know least about possible mechanisms. How excitation energy is first fixed in a chemical form remains a problem. Reduced coenzyme may represent the final product of a whole sequence of hydrogen transfers interposed after the water-splitting. A search is now in progress to find whether any carriers or specific catalysts concerned in such a transfer can be isolated from green plants. Hill and his collaborators [14] have isolated, in impure form, a protein which permits hydrogen transfer from the chloroplast system to addition reagents which are inert in the absence of the protein.

In a stimulating, but speculative, discussion Warburg [15] has suggested that a carotenoid acts as a hydrogen carrier between water-splitting and

the reduction of coenzyme. This view is based on experiments in which it was shown with *Chlorella* that the photosynthetic efficiency in red light was apparently increased by previous exposure to blue-green light; further, inhibition of photosynthesis by *o*-phenanthroline—a metal-chelating agent—was overcome by illumination with blue-green light. Warburg interprets these observations in terms of *Photosynthese-Fermente*, probably containing metal groups, which are preferentially activated by blue-green light. Many further observations must be made to test this hypothesis.

Physiological investigations relevant to this matter are those which determine the photosynthesis resulting from very brief light-flashes [16]. If *Chlorella* is illuminated by flashes of less than 10^{-4} second duration, the oxygen evolved depends on the length of dark-time between flashes, and reaches an asymptotic value independent of the intensity of the flash. Thus there is a limited amount of energy which can be fixed during a single flash; this may be due to a limited amount of carrier substance which, once charged up, must be allowed sufficient dark-time to discharge before it can be charged again. The amount of this substance corresponds to one molecule per two thousand molecules of chlorophyll. The chemical identity of this carrier is not known.

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The history of garden roses

ANN WYLIE

The rose is unique among garden flowers—unique in its universal appeal and its seemingly endless variety of form and colour. Yet, although there are over a hundred species of wild roses, the great majority of the varieties now grown are derived from only six of them. This article reviews the origins of roses and the principal methods used in their development, and the underlying genetic principles, understanding of which is enabling the work increasingly to be put on a systematic rather than its formerly wholly empirical basis.

The early history of garden roses, like that of so many groups of cultivated plants, is obscure. However, as M. B. Crane [1] has shown, modern genetical and cytological studies can give us a clear understanding of the way in which the present-day cultivated varieties of, for instance, wheat, tobacco, strawberries, and plums must have been developed. The same type of study has yielded much information on the origin of many groups of ornamental plants.

The chief processes concerned in this evolution have been classified by Crane under the following headings: (*a*) Gene mutation. (*b*) Simple autopolyploidy, that is, chromosome doubling in a normal non-hybrid plant: this frequently results in increased flower-size and substance, as in the recently introduced artificial tetraploids of Antirrhinum and Salvia. (*c*) Interspecific hybridization. (*d*) Interspecific hybridization accompanied by chromosome doubling (allopolyploidy). Most interspecific hybrids show varying degrees of sterility, and doubling the chromosome number of such hybrids frequently brings about a restoration of fertility, as well as the general increase in size due to polyploidy. Examples of all these types of change can be seen in the development of the garden roses of today. As C. C. Hurst [2] and others have pointed out, this development can conveniently be considered in two parts, one prior to 1800, during which the groups of so-called old-fashioned European roses came into being, and the second, from 1800 to the present day, which began with the introduction to western Europe of perpetual-flowering roses from the Far East.

There is comparatively little precise knowledge of how the various groups of old-fashioned roses developed. Hurst gives an admirable summary of the available data. The most important ancestral species for all the groups is *Rosa gallica*, the French Rose, indigenous in southern Europe and western Asia. Figure 1 is taken from Redouté's great work, *Les Roses*, and shows a single-flowered form of *R. gallica* which is probably very close to the wild species. The species is a tetraploid with twenty-eight chromosomes, as are the cultivated *gallica* varieties and also the very closely related groups of Damask, Centifolia, and Moss Roses. *R. gallica* is an immensely variable species, and numerous mutations affecting, in particular, the colour and degree of doubleness of the flower have been preserved in cultivation until this day. It is also very fertile, and many varieties were produced by hybridization of distinct forms and by selection among the progeny. Deliberate hybridization did not start until the eighteenth century, when Dutch, and later French, horticulturists took part in the work. Early in the nineteenth century more than a thousand varieties were known, though few still survive.

The origin of the cabbage roses (Centifolias), is unknown. *R. gallica* is undoubtedly one of the ancestral species, and, like this species, almost all the Centifolia varieties are tetraploids. The first, dating from the early eighteenth century, were completely double-flowered, with all the stamens converted into petal-like structures and with imperfectly developed carpels. It was therefore impossible to breed from them, and for a long time the sole source of new varieties was bud mutation, that is, a gene mutation occurring in a somatic cell. If this occurs sufficiently early in the development of a bud, then the greater part of the shoot later produced may have the altered genetic constitution. At the beginning of the nineteenth century a single-flowered mutation occurred which made hybridization with other groups possible. One of the notable mutations in the Centifolias is that which was responsible for the development of the moss character. This involved the formation of complex glandular hairs on flower stalk, ovary wall, and sepals, extending in some moss roses to the young stems and leaves as well.

The small group of Alba varieties, which includes the white rose of York, is much more distinct than are the other European rose groups. The Albas are hexaploids, with 42 chromosomes, and the group originated through some chance hybridization between one of the white-flowered dog roses (whose female gametes contain 28 chromosomes) and *R. gallica*.

All these old European roses had but one period of flowering, in early summer, except for a few damask varieties which produced a sporadic crop of flowers in the autumn. However, perpetual-flowering roses occur in the section Chinenses of the genus. This contains the diploid species *R. chinensis* from China and *R. gigantea* from Burma; figure 4 is an illustration of the latter from Ellen Willmott's 'The Genus *Rosa*.' The Chinese had been growing roses for many centuries when regular trade with the West became established in the eighteenth century, and it was cultivated Chinese roses, probably many generations removed from the wild *R. chinensis* and *R. gigantea*, that were then brought back to England. Only four of these introductions seem to have taken part in the subsequent development of our modern roses, and a full description of these 'Stud Chinas' is given by Hurst [2]. Two are shown in figures 7 and 2: *R. semperflorens* (introduced in 1792) from an illustration in an early number of Curtis's *Botanical Magazine*, and 'Parsons' Pink China' (1793), from Redouté. The remaining two varieties, now extinct, showed a preponderance of characters from *R. gigantea*, and these, respectively pale pink and pale yellow in colour, played a prominent part in the development of the tea roses.

Very soon after the establishment of the Chinese roses in Europe, hybridization with the existing European roses began. A number of stages in this process can be distinguished. The first crosses resulted in two very distinct groups, the Noisettes and the Bourbons. The former came from a cross between the Pink China and the Musk Rose *R. moschata* (illustrated in figure 3, from Redouté). This diploid species is a climber with clusters of sweetly scented flowers, and is fairly closely related to *R. chinensis*. The initial hybrid, raised in America, was summer-flowering like the musk rose, the perpetual-flowering gene being recessive. However, in later generations bred by M. Noisette in France recombination yielded perpetual-flowering derivatives, one of which is shown in figure 5, from Redouté. These early Noisette varieties were also back-crossed to the Chinese roses, producing plants with larger flowers, more like the Tea roses. Some of these, such as Maréchal Niel and William Allen Richardson, are still grown today. The Noisettes are diploids like their ancestral species.

The Bourbon group stemmed from an accidental cross between the Pink China and an old damask rose which occurred about 1815 in Réunion Island, then known as l'Île de Bourbon. A group of vigorous shrub roses with large, beautifully scented flowers developed from crosses of the original hybrids with the Gallicas and damasks. One of the early varieties is shown in figure 6, from Redouté. Bourbons still grown today include Souvenir de la Malmaison, Zephyrine Drouhin (both triploids), Louise Odier, and Madame Pierre Oger (tetraploids). Bourbon roses were also concerned in the development of the later group of Tea roses, since many of the pink tea varieties trace back to a cross between a Bourbon and a derivative of *R. gigantea*. Further development in the Tea rose class came from intercrossing these Bourbon-teas with the Noisette-teas referred to above. Between 1850 and about 1890 this yielded many varieties noted for their abundance of large, beautifully formed, and highly scented flowers. But these tea roses were not especially hardy in England and northern Europe. Well known varieties are Marie van Houtte, Safrano, and Perle des Jardins, while the climber Gloire de Dijon is intermediate between the Noisette and Tea rose classes.

The important Chinese introductions were also crossed directly with Gallicas and other European roses, yielding the so-called Hybrid Chinas, summer-flowering shrub roses prominent in the first half of last century. These were mainly triploids and hence very sterile, but an important 'break' occurred about 1830 with the appearance of fertile tetraploids, for example Malton and Athalin. Interbreeding of these tetraploid hybrid Chinas with the later Bourbon varieties (also tetraploid) and the Portland roses (a small group originating from *R. chinensis* and Autumn Damask) produced the somewhat heterogeneous collection of roses known as Hybrid Perpetuals, which were widely grown, along with the tea roses, in the second half of last century. They were hardy shrubs with, despite their name, only a limited second flowering in the autumn in most varieties. Famous Hybrid Perpetual varieties include Général Jacqueminot, La Reine, and Frau Karl Druschki.

The Tea and Hybrid Perpetual classes therefore each had rather serious limitations, and it was

FIGURE 1 – Rosa gallica rosea (*flore simplici*). *From* Les Roses, *by P. J. Redouté, text by C. A. Thory. Folio edition. Published by Firmin Didot, Paris,* 1817–24. *Vol.* 3. (*Original plate slightly larger.*)

FIGURE 2 – Rosa indica vulgaris. *From* Les Roses, *by P. J. Redouté. Vol.* 1. (*Original plate approximately twice this size.*)

FIGURE 3 – Rosa moschata. *From* Les Roses, *by P. J. Redouté. Vol.* 1. (*Original plate approximately twice this size.*)

FIGURE 4 – Rosa gigantea (*original painting*). *From* The Genus Rosa, *by Ellen Willmott, F.L.S., drawings by Alfred Parsons, R.A. Vol.* 1, *Plate* 34. *Published by John Murray, London,* 1914. (*Original plate approximately twice this size.*)

FIGURE 5 – Rosa Noisettiana. *From* Les Roses, *by P. J. Redouté. Vol.* 2. (*Original plate approximately twice this size.*)

FIGURE 7 (*right*) – Rosa semperflorens. *From* The Botanical Magazine, *by William Curtis.* 1794. *Vol.* 8, *Plate* 284. (*Original plate approximately same size.*)

FIGURE 6 (*above*) – Rosa canina Bourboniana. *From* Les Roses, *by P. J. Redouté. Vol.* 3. (*Original plate approximately twice this size.*)

FIGURE 8 (*right*) – Rosa lutea. *Single yellow rose. From* A Collection of Roses, *by Miss M. Lawrance.* 1799. *Published by herself. Plate* 12. (*Original plate approximately twice this size.*)

natural that attempts should be made to obtain, through hybridization, a race which combined the good qualities of the two. This was first achieved by the French breeder M. Guillot, who in 1867 introduced the variety La France, forerunner of the Hybrid Tea class, the dominant garden roses of this century. La France itself is a triploid, as is to be expected for the product of a cross between a diploid tea rose and a tetraploid hybrid perpetual. These early triploid hybrid teas were rather sterile, like the first Bourbons and hybrid Chinas before them. For the first twenty-five years or so, new hybrid tea varieties were obtained mainly by repeating the tea/hybrid perpetual cross using different parental varieties. Then, towards the turn of the century, tetraploids appeared, probably through the functioning of unreduced gametes, i.e., pollen grains and embryo sacs containing the same number of chromosomes as the somatic cells, instead of half that number. This is brought about through the failure of one or other of the two divisions of meiosis. One of the first tetraploids was the well known Caroline Testout, and in these fertility was restored. A period of very rapid production of new varieties followed as a result. The hybrid teas soon usurped the position formerly occupied in gardens by their ancestors the hybrid perpetuals, largely on account of their more continuous flowering season. Their great advantage over their other ancestors, the tea roses, lay in their comparative hardiness.

The colours of the early hybrid tea varieties ranged from deep red, through pink, to white. There were no good yellow varieties. The development of these had to wait on the introduction of a new species into the garden roses. This occurred at the beginning of this century when M. Pernet-Ducher, the famous French breeder, obtained a hybrid between the Persian yellow rose *R. foetida* (formerly *R. lutea*, see figure 8) and one of the hybrid perpetuals. *R. foetida* is a tetraploid like the hybrid perpetuals and the later hybrid teas. It flowers only once, in early summer, like most rose species. The original hybrid when crossed with a hybrid tea produced the first really yellow variety, Soleil d'Or, from which came the so-called Pernetianas. These were characterized not only by their brilliant yellow and orange colours but also, unfortunately, by lack of fragrance, susceptibility to the fungal disease black spot, and the excessive thorniness of their *R. foetida* ancestor. Repeated crossing with good hybrid tea varieties, and careful selection during the next twenty-five years, led, however, to the elimination of most of the faults brought in by *R. foetida* and also to the complete merging of the Pernetianas with the Hybrid Tea class proper. There are very few hybrid tea varieties bred today which do not trace back through one or other of their parents to Soleil d'Or or one of the other early products of the cross with *R. foetida*.

No further species have been involved in breeding hybrid teas up to the present, so that the members of this now very large group have the following species as ancestors: *R. chinensis*, *R. gigantea*, *R. moschata* (diploids), *R. gallica*, and its ancient derivatives, and *R. foetida* (tetraploids). This is schematically shown in figure 9.

A much less important group of garden roses was developed at about the same time as the hybrid teas. This had its origin in crossing *R. chinensis* with another Far Eastern species, *R. multiflora*, which is a diploid climber with enormous clusters of small, white flowers. In the second generation dwarf plants appeared which produced clusters of flowers all the summer, and from these ancestral varieties, Mignonette and Paquerette,

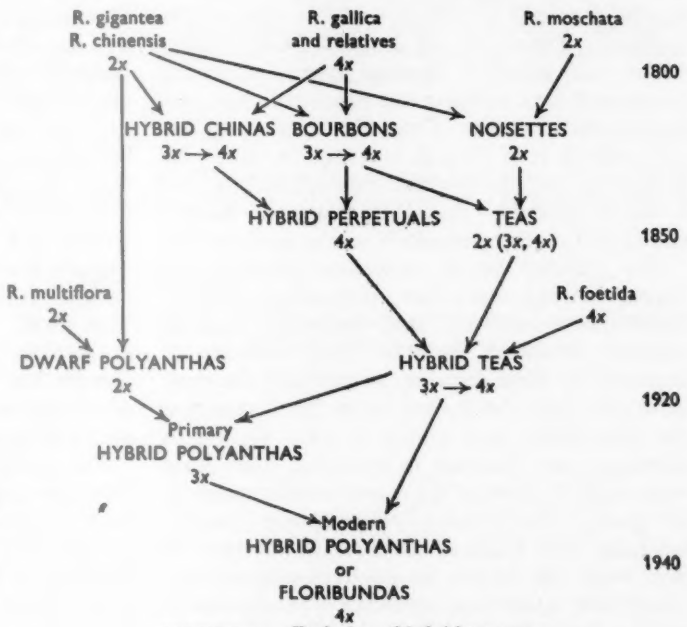

FIGURE 9 – *Evolution of hybrid tea roses*

was developed the Dwarf Polyantha class (*R. multiflora* at that time being known as *R. polyantha*). Later varieties include Orleans Rose, Gloria Mundi, and Coral Cluster. The Dwarf Polyanthas are all diploids, like their ancestral species. Many varieties in this group have arisen by bud mutation, one of which deserves mention, since it made possible a considerable extension of the colour range in the garden roses. It determined the production of the anthocyanidin pigment pelargonidin in place of cyanidin, the usual pigment in *Rosa* (see Robinson [3] for an account of the anthocyanins and anthoxanthins). Pelargonidin is responsible for the brilliant orange colour of the dwarf polyantha variety Paul Crampel and several others, a colour unknown in garden roses before about 1930.

The Danish breeder Poulsen created a further class by crossing these diploid dwarf polyanthas with the tetraploid hybrid teas in an endeavour to produce a race of really hardy roses with large flowers, suitable for outdoor cultivation in the rigorous climate of northern Europe. In this he was brilliantly successful. The new Hybrid Polyantha class which came into being about 1920 combined the hardiness, long flowering period, and cluster-flowered habit of the dwarf polyanthas with the larger flower size and more elegant shape of the hybrid tea. The early varieties, such as Else Poulsen, are triploids and rather sterile. However, the tetraploid level was regained following back-crosses to the hybrid tea side of the pedigree. Examples are Donald Prior, Dainty Maid, and Maid of Honour (syn. Schleswig). Continued back-crossing has resulted in the production of a number of varieties in the past few years which it is difficult to place in either the Hybrid Tea or the Hybrid Polyantha class, and it seems probable that these formerly distinct classes will merge completely in the next decade.

The primary hybrid polyantha varieties are almost scentless, and rather susceptible to mildew, undesirable characters both inherited from *R. multiflora*. However, the more recent varieties are improved in these respects, particularly the roses in whose origin derivatives of the musk rose and the sweet briar have played a part. Kordes in Germany, and Boerner in America, have been responsible for most of the recent developments in this group. The varieties Independence (Sondermeldung) and Fashion are notable examples of their work: the former for its vivid cinnabar-red colour (due in part to the presence of pelargonidin) and the latter for its delicate coral-peach shade.

There are many other groups of garden roses of lesser importance, some of which deserve to be mentioned briefly (a more detailed account may be found elsewhere [4]). Climbing roses are of a number of distinct types. The Noisettes and climbing tea roses have been noted above. Towards the end of last century hybrids between *R. multiflora* and China roses, Noisettes, and other groups gave rise to the class of Multiflora ramblers which includes Tausendschön and Veilchenblau, with its near-purple flowers. However, a superior group of climbers came from the use of a new species, *R. wichuraiana* from Eastern Asia. Its hybrids have a longer flowering period than do the Multiflora ramblers and are much less susceptible to mildew than the latter. Widely grown varieties include Albertine, Emily Gray, Paul's Scarlet, and Chaplin's Pink. The other important group of climbers consists of climbing sports of the ordinary bush hybrid tea varieties. These are identical with the parent bush variety except in the climbing habit. Unlike the Multiflora and most Wichuraiana varieties which flower for a few weeks only, the climbing hybrid teas produce a succession of flowers throughout the season. Climbing Crimson Glory and Climbing Mrs. Sam McGredy are two of the most reliable varieties, many of which are prone to revert to the bush habit.

There are a number of distinct types of shrub roses which deserve to be more widely grown. One group contains the hybrids of *R. rugosa*. They are very hardy, remarkably resistant to disease, and have a prolonged flowering season. Commonly grown varieties include Belle Poitevine, Roseraie de l'Hay, and Conrad Ferdinand Meyer. *R. rugosa* belongs to quite a different section of the genus from the other ancestral species, and Rugosa hybrids are extremely sterile. This has proved a barrier to further breeding work, which has only recently been overcome through the spontaneous occurrence of chromosome doubling in the diploid Max Graf. The tetraploid so formed, known as *R. kordesii*, is fertile, and the German breeder Kordes has recently produced hybrids from it which approach closely the ideal of a hardy, perpetual-flowering climber.

The hybrid musk roses are excellent shrubs. They are a development from the old Noisettes, through crossing with hybrid teas and other groups, and are largely the result of the work of Lambert in Germany and of Pemberton in England. Some well known varieties are Penelope, Prosperity, and Nur Mahal. They produce

clusters of sweetly scented flowers all through the summer and autumn. Some hybrid musks have been important in the development of hybrid polyantha-like roses, and many modern cluster-flowered varieties are complex derivatives of combined hybrid polyantha, hybrid musk, and, in some instances, hybrid sweetbriar origin. Examples are Grandmaster, Rudolph Timm, and Cocorico.

The native sweetbriar, *R. rubiginosa*, is one ancestor of the Penzance Briars, produced at the end of last century by Lord Penzance from crosses with the hybrid perpetuals and *R. foetida*. Many were named after Scott's heroines, such as Lucy Ashton, Flora McIvor, and Anne of Geierstein. They retain the sweetly scented foliage of *R. rubiginosa* and have semi-double bright flowers and attractive hips. Derivatives of the Penzance Briars have recently been used by Kordes in breeding cluster-flowered roses, and some of these are notably resistant to the fungal disease black spot.

A final group of shrub roses that may be mentioned has the Scotch or Burnet rose, *R. spinosissima*, as an ancestor. This recent development also is due to Kordes, who crossed the species with hybrid teas and obtained several early flowering shrub roses of considerable merit. These include Frühlingsgold, with double yellow flowers, and Frühlingsmorgen, with large single flowers whose petals are yellow at the centre shading to a vivid pink at the edges.

This brief survey shows that the most important factor concerned in the evolution of the cultivated roses has been interspecific hybridization and, more recently, hybridization between the different groups formed by the earlier crosses. Polyploidy has been significant in some classes in raising initially diploid and triploid members of a group to the tetraploid level of some of their ancestral species. This has undoubtedly facilitated gene exchange in this century between the different rose groups and has led to the disappearance of the boundaries between formerly distinct classes.

Although the genus *Rosa* is a very large and diverse one, with over one hundred species in the North Temperate zones of both New and Old Worlds, only six of these have been used in the development of the important rose groups discussed in this article. A further eight have been concerned in minor developments, some of which have been briefly considered. The remaining ninety per cent of the genus contains many desirable species which have much to offer the breeder of garden roses, as inspection of the National Rose Species Collection at the John Innes Horticultural Institution will show. Fortunately, enterprising breeders on the Continent and in the United States have been using some of these neglected species in their programmes with, in some cases, very promising preliminary results. But there are many problems of sterility to be overcome and much basic genetical information yet to be acquired.

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Problems of phyllotaxis and leaf determination

R. SNOW

The study of the disposition of leaves on the stem is not only of intrinsic interest, but may well throw light on the fundamental problem of what causes leaf formation. Inferences made from observations of already elongated shoots can be misleading. In this article the problems of phyllotaxis are discussed on the basis of observation of exposed stem apices and transverse sections of buds, in which the relative positions of young leaves are still almost unchanged and can be fairly accurately measured, and of operations on stem apices.

Leaves arise as rudiments or primordia, round or nearly so, from the surface of a narrow zone forming a ring just below the summit of the bare stem apex (figure 1). The stem apex is commonly paraboloidal, steeper in some species and flatter in others, but the zone from which the leaves arise approximates to part of the surface of a cone. The leaves arise nearly always in regular positions, so that they form regular patterns, simple in some species and complicated in others. Clearly one problem is what causes a leaf to arise at all; a similar problem is posed by the outgrowth of lateral branches from various filamentous algae and fungi. But a second problem is what causes leaves to arise in regular positions around the apex, since these positions, when first determined, do not correspond to any obvious differentiations within the apex. In this respect the origin of leaves differs from that of lateral roots, which originate below the surface just externally to the first-formed xylem strands. It has, indeed, been suggested that the positions of the leaves depend on those of the conducting strands supplying them, or of some invisible precursors of those strands, but the experimental evidence excludes this in the species tested [1]. The problem of the causes determining the position of the leaves is a challenge, since the regularity of their positions must, like any other facts of differentiation, have a rational explanation. But the study of the location of leaves may also prove to be a useful, though indirect, way of approaching the fundamental question of what causes them to originate at all.

The positions in which the leaves are formed at the apex are the primary factor determining the positions which they later occupy along the main stem, but during the elongation of the stem their relative positions are often changed in various ways. These secondary changes have their own interest, but they present problems quite separate from that of the positions in which the leaves are formed. Nevertheless, the study of phyllotaxis was at first based on observations made on elongated shoots; even now the positions in which leaves have arisen are sometimes inferred from observations of this kind. But such inferences are extremely unreliable, because of the changes that take place during the elongation. In the present paper the problems of the determination and primary location of leaves will be discussed on the basis of observations and experiments made directly on exposed stem apices, and of observations of transverse sections of buds, in which the angular positions of the young leaves can be measured fairly accurately and have not yet changed appreciably.

There are many interesting kinds of phyllotaxis, but here we shall discuss only the commonest kind, the spiral, which raises probably the most interesting questions of all. Two other common kinds will, however, need to be mentioned. One of these is the distichous or two-ranked system (figure 2); this is well known in grasses and in some common *Leguminosae*, including peas and beans. In this system each leaf arises singly and at an angle of 180° from the previous one, so that the leaves form two opposite ranks, which appear radial in bud sections and vertical on the elongated shoot. The other kind is the decussate, or crossed, system (figure 3), found for example in ash, horse-chestnut, and *Labiatae*. In this the leaves arise two at a time, the members of each pair being opposite and in a plane at right angles to that of the previous pair, so that the leaves form four radial or vertical ranks.

Spiral phyllotaxis is found in most flowering

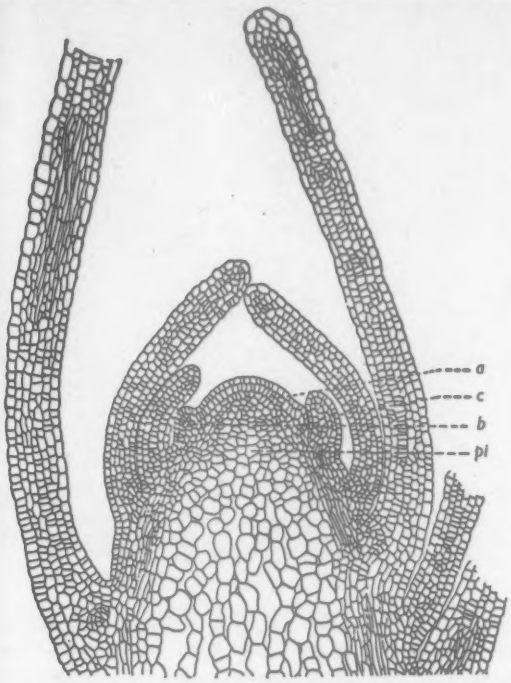

FIGURE 1 – *Median longisection of the stem tip of* Linum, *showing several stages in the ontogeny of the leaf:* a, *section of a very young leaf primordium;* b *and* c, *older primordia, showing early development of provascular strands;* pi, *pith.* (*After Crooks*, 1933.)

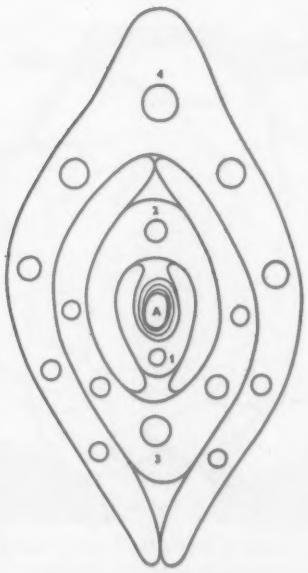

FIGURE 2 – *Transection of distichous apical bud of* Bupleurum perfoliatum. A, *apex;* 1–4, *successive leaves.* (*After van Iterson.*) (× 127)

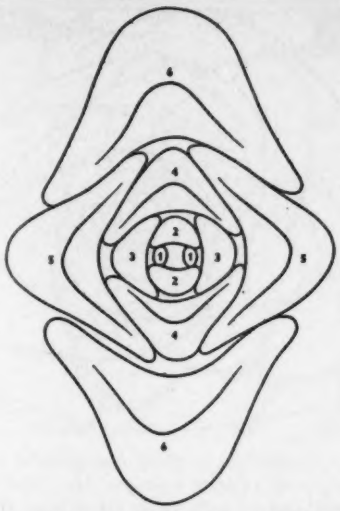

FIGURE 3 – *Transection of decussate apical bud of* Syringa vulgaris. 1, 1 *and* 2, 2, *etc., successive pairs of leaves.* (*After van Iterson.*) (× 45)

plants and conifers, in most ferns, in many lycopods, and in most mosses, though in mosses it is of rather a special kind. The common property of the spiral systems is that a single spiral, called the ontogenetic or genetic spiral, can be drawn through the centres of all the leaves in their order of succession, and that the angles between successive leaf centres are as a rule very nearly constant.

An obvious difference between various spiral systems, and one useful for classification, is that in some the buds contain a small number of relatively large leaves around the apex, and in others a larger number of relatively small leaves (figures 4–6). The former condition is called 'low', and the latter 'high', phyllotaxis. One way of expressing this difference precisely is to count in transections of buds the numbers of certain curves—called the parastichies, or contact parastichies—which are formed by adjacent leaf-bases. There are usually two sets of these curves winding in opposite directions round the apex; they can be seen in figures 4–6, especially clearly in figure 6. In some species there are three sets of such curves (figures 9 and 10).

It is found that the numbers of contact parastichy curves in the two or three sets are nearly always successive terms of the summation series 1, 2, 3, 5, 8, 13; this is the Fibonacci series, in which each term after the first two equals the sum of the previous two. Thus T. Fujita [2], examining vegetative buds of 435 species of angiosperms and 45 of gymnosperms with spiral

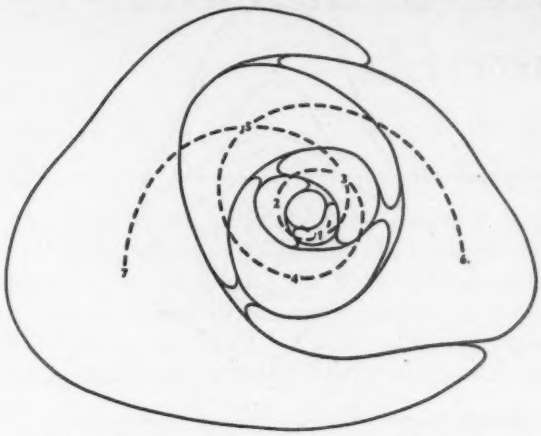

FIGURE 4 – *Transection of apical bud of* Bellis perennis. *Parastichy or contact numbers* 1 *and* 2. *The single parastichy curve is drawn, and one curve of the set of two. Both curves start at leaf* 1. (*After van Iterson.*) (× 36)

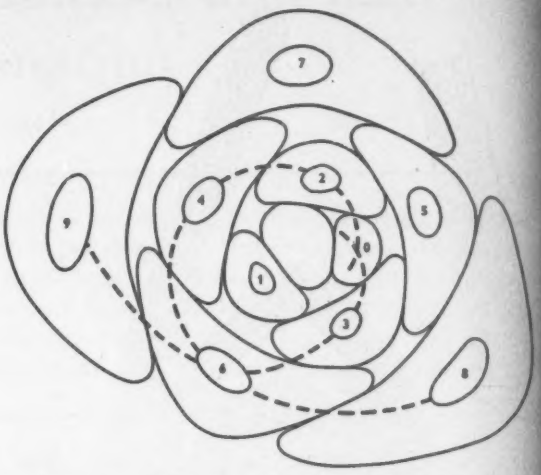

FIGURE 5 – *Transection of apical bud of* Jasminum fruticans. *Parastichy or contact numbers* 2 *and* 3. *One parastichy curve of each set is drawn, starting at leaf* 0. (*After van Iterson.*) (× 103)

phyllotaxis, found Fibonacci parastichy numbers in all except one angiosperm and one gymnosperm. The commonest pairs of numbers were 2 : 3 and 3 : 5. In the lowest spiral phyllotaxis one parastichy set contains only one curve, which is then the same as the ontogenetic spiral (figure 4). Some of the highest Fibonacci numbers of parastichies are found in the large, flat inflorescences of sunflowers. Figure 7, from A. H. Church [3], shows one with parastichies 55 and 89, and Church has also shown another with parastichies 89 and 144.

Even when the parastichy numbers do not follow the Fibonacci series they regularly belong to some other summation series, usually to the subsidiary series 1, 3, 4, 7, 11, etc. (figures 8 and 9). Examples of still other summation series are known, for instance 1, 4, 5, 9, etc., and 2, 5, 7, 12, etc. [4]. These remarkable facts call for explanation.

In practice, it is often more convenient to find these numbers in a way slightly different from that previously described. One numbers successive leaves in a bud section along the ontogenetic spiral, and then counts how many intervals, or plastochrons, have intervened between the formation of any leaf of the top cycle, and of the two or three adjacent leaves below it. These numbers are called the contact numbers, or contacts, since in flowering plants (though not in ferns) the bases of adjacent leaves are nearly always in contact in the bud. They are the same as the parastichy numbers where there are enough leaves to form parastichies, and they can be found even when there are not. Another way of classifying spiral systems according to their lowness or highness, less simple but more finely graded, has been proposed by F. J. Richards [5, 6]. The higher Fibonacci spiral systems are developed gradually from very low systems. The simplest developments are found in the seedlings of dicotyledons, and examples will be described and discussed later.

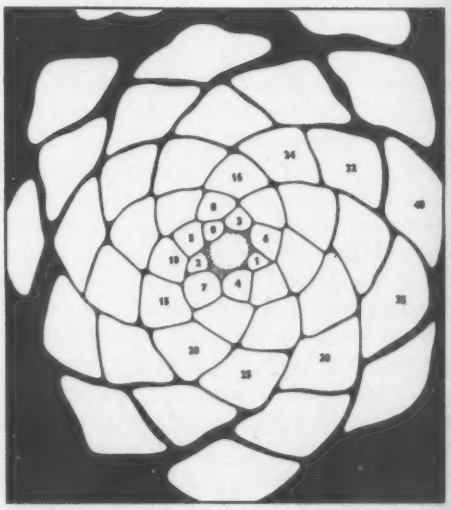

FIGURE 6 – *Transection of apical bud of young seedling of* Pinus pinea. *Parastichy or contact numbers* 5 *and* 8. *The youngest* 8 *leaves are numbered, and also those along one parastichy of each set, starting at leaf* 0. (*After Church,* 1920.)

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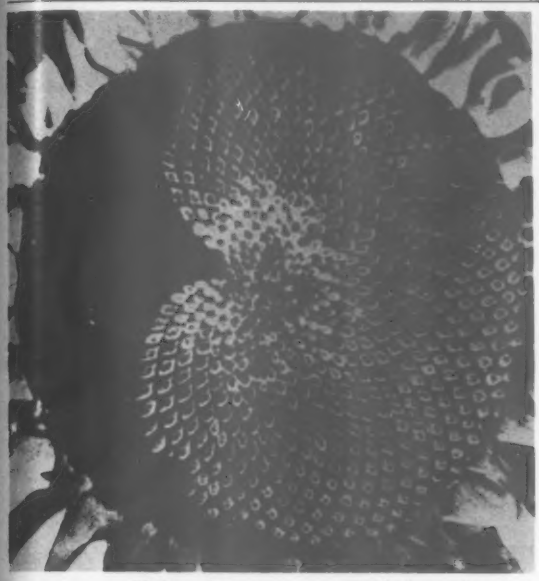

FIGURE 7 – Helianthus annuus. *Capitulum selected as a type. Contact-parastichies* (34 + 55)*; fruits partially removed to show the direction of the curves.* (*After Church,* 1901.)

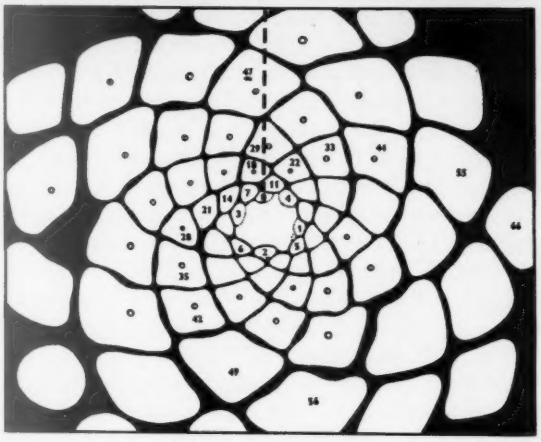

FIGURE 8 – *Terminal bud of branch of* Araucaria excelsa. *Parastichy or contact numbers* 7 *and* 11. *The leaves are numbered along one parastichy of each set. The line drawn outwards from leaf O is explained in the text.* (*After Church,* 1920.)

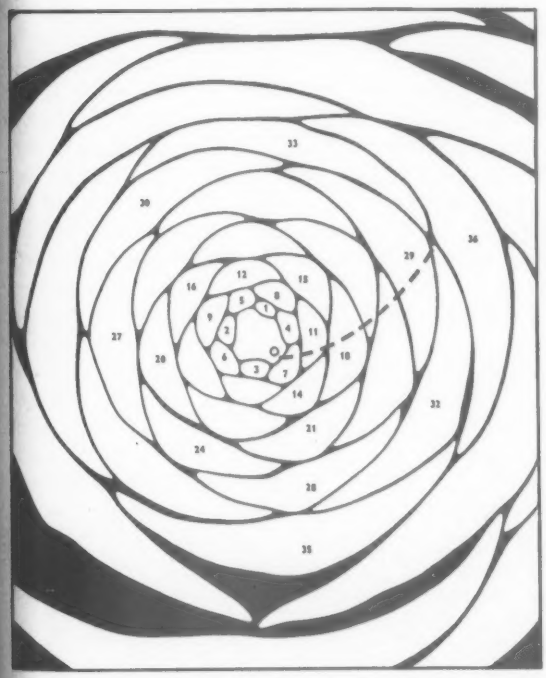

FIGURE 9 – *Apical bud of* Euphorbia biglaendulosa. *Parastichy or contact numbers* 3, 4, *and* 7. *The leaves are numbered along one parastichy of each set. The curved line is explained in the text.* (*After Church,* 1901.)

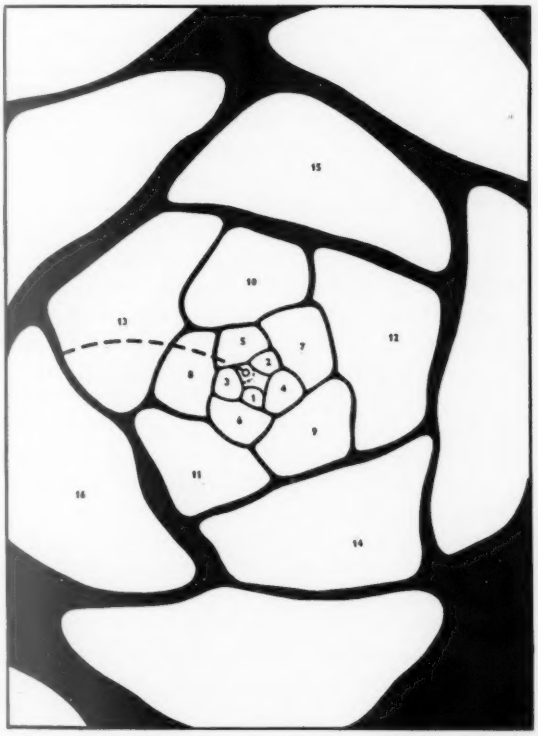

FIGURE 10 – *Apical bud of* Sedum acre. *Parastichy or contact numbers* 2, 3, and 5. *The curved line is explained in the text.* (*After Church,* 1901.)

DIVERGENCE ANGLES

Study of the divergence angles between successive leaves in spiral systems has revealed equally remarkable facts, but in this connection it is necessary first to consider the famous theory of Schimper and Braun [7], which unfortunately has obscured the truth for 120 years. These authors proposed the rule that the divergence angles are normally rational fractions of 360° and that, while in distichous phyllotaxis the divergence is $\frac{1}{2}$, in spiral phyllotaxis the fractional divergence is usually some later member of the series $\frac{1}{2}$, $\frac{1}{3}$, $\frac{2}{5}$, $\frac{3}{8}$, etc. From this it would follow that one leaf can be found exactly above another, or with its centre on the same radius as seen in bud sections, after a number of divergence angles along the spiral equal to the denominator of the appropriate fraction. Unfortunately they did not measure the angles in bud sections near the apex, but on mature shoots, where it is very difficult to measure accurately and where the original angles have often changed. They found what they supposed to be exactly superposed leaves, and calculated the mean value of the intervening divergence angles.

However, measurements of these angles in sections of buds with Fibonacci spirals do not support the proposed rule in any way. The angles do not fall into groups corresponding even approximately with the Schimper-Braun fractions. Indeed they do not fall into any groups whatever, but in these spirals are very close to the Fibonacci angle itself. This angle, 137° 30′ approximately, is that subtended by a fraction of the circumference equal to the limiting value to which tend the fractions of the Schimper-Braun series. This value differs very definitely from the Schimper-Braun values $\frac{1}{3}$ or 120°, $\frac{2}{5}$ or 144°, $\frac{3}{8}$ or 135°, though the later values of this series of fractions approach it closely.

This is shown most clearly in another valuable paper by Fujita [8], who measured numerous divergence angles, to the nearest degree, in bud sections of thirty species of flowering plants having various Fibonacci parastichy numbers; he usually measured from 100 to 500 angles in each species. He recorded the frequency distributions of these angles. The distributions for all the species have sharp peaks, the maxima at either 137° or 138°. In one conifer having parastichies 3 and 4, belonging to the series 1, 3, 4, 7, etc., the peak of the frequency distribution was at 100°; in the bud of *Araucaria excelsa* (Church [14]), shown in figure 8, the mean of forty-seven angles is 99·8°. Both these values are very close to 99° 30′, the limiting angle of the corresponding series of fractions. In another conifer having parastichies 2 and 5, belonging to the still rarer series 2, 5, 7, 12, etc., Fujita [4] found the peak of the distribution at 151°, again very close to the limiting value 151° 8′.

From these striking results it follows that in spiral systems the leaves commonly considered to be superposed are not really so. It can, indeed, easily be seen in transections of spiral buds that lines drawn through the centres of such leaves, lines forming the so-called orthostichies, are not straight but have a slight and regular curvature in the same direction. This is the easiest way of verifying that in buds the actual divergence angles depart systematically from the Schimper-Braun fractions. The only known exceptions are various succulent species, in which, when the stems develop vertical ridges, the ridges continue up into the stem apex, and then apparently promote the formation of leaves which are formed along them [9]. Fibonacci spirals cannot be classified according to their divergence angles, since these angles are practically the same in all of them, apart from special cases.

However, some observers have stated that in the mature shoots of some, though by no means all, species, the orthostichies are more nearly straight than in the bud, or even quite straight. Such statements are difficult to verify, but in so far as they are true, the explanation is probably that given by P. Teitz [10]. This is that the conducting strands commonly join up along the orthostichies, which are at first curved, being really helices. Later, however, the strands tend to elongate less rapidly than the rest of the stem, and so set up a resistance and get pulled more nearly straight, thereby twisting the whole stem, straightening the orthostichies, and causing the angles on the mature stem to approach the Schimper-Braun values. Such secondary changes are irrelevant to the problem of the primary location of leaves.

Although Fujita's measurements of divergence angles are the most numerous, several earlier workers had also published measurements of divergence angles and other evidence showing that the angles do not conform to the Schimper-Braun rule. The brothers L. and R. Bravais [11] maintained this very convincingly as early as 1837, and so also, more recently, did Church [3] and M. Hirmer [12, 13]. The Bravais, Hirmer, and Church [14] found further that the actual angles are close to the limiting value of the series, even

though the Bravais made their observations on mature shoots. Yet even now the Schimper-Braun fractional divergence angles are often quoted in discussions of phyllotaxis in buds, as if they were genuine.

THEORIES OF LEAF DETERMINATION

In attempting to interpret the main facts so far recorded, one needs some theory of leaf determination as a working hypothesis. Such theories can be tested for their agreement both with observations of naturally growing plants and with the experimental results now available from operations upon stem apices or the youngest leaf primordia. Only a few theories will be discussed here, and mainly those that are attracting interest at present.

Schimper and Braun supposed that some leaf-forming impulse moved along the ontogenetic spiral, but there is plenty of evidence that the ontogenetic spiral has in general no causal significance. For instance, in the inflorescence heads of Compositae, one side may cease to grow, so that the ontogenetic spiral is lost, but yet the phyllotaxis may continue fairly regularly on the other side [15]. The spiral can also be reversed experimentally [16, 21].

A very different theory of leaf-forming impulses was put forward by Church [3, 14]. He supposed that such impulses moved centrifugally along two sets of intersecting curves, which wound round the stem apex and were continuous with the leaf-parastichies below. New leaves were supposed to be formed at the intersections of the curves [14].

Another parastichy theory has been proposed recently by L. Plantefol [17, 18], and has found much favour in its country of origin. He supposes that leaf-forming influences travel from below upwards into the leaf-forming zone of the apex along one set of curves, which he calls foliar helices. These curves are the parastichies of one of the two intersecting sets, at least in low phyllotaxis systems of dicotyledons, where they are supposed to be regularly two in number. In higher systems the foliar helices are supposed to branch, and in distichous dicotyledons it is not clear what they are supposed to be. The choice of one set of parastichies only is arbitrary, since there is no valid reason for preferring one of the two intersecting sets to the other. This is especially obvious in the symmetric distichous and decussate systems (figures 2, 3), in which the two sets are alike. The theory would make it very difficult to account for the observed constancy of the divergence angles along the ontogenetic spiral, especially after a change in the number of parastichies, as Richards has clearly explained [6]. For after such a change, the angle between subsequent leaves along each of the foliar helices would need to be changed correspondingly.

The experimental evidence also is against the theory. In many operations made on apices of the common fern by C. W. Wardlaw, and on *Lupinus albus* by M. and R. Snow, two species having Fibonacci spirals, no indication has been found that leaf formation is promoted in the slightest by any influence deriving from existing leaves along either set of parastichies. Yet several of these experiments would have revealed such an influence if it had existed. For example, in the common fern Wardlaw [19] found that the next three leaf primordia due to arise, I_1, I_2, and I_3, were formed normally even when their presumptive areas were confined between two radial cuts which, as his drawings show, quite separated each of them from the older primordia of both of the intersecting parastichies to which it belonged. Further, I_2 is not yet determined at the time of operation, as is shown by other experiments by Wardlaw [20].

In *Lupinus albus*, M. and R. Snow [21] made a radial cut through the presumptive area of I_1, approximately in its median plane, and extending well below that area. Sometimes a newly determined leaf arose with its side abutting on one side of the wound—the uphill or anodic side in relation to the ontogenetic spiral—and sometimes it arose abutting on the other—the downhill side of the wound. In one or other of these two groups of results this new leaf must have been determined when quite cut off from the older members of its foliar helix, to whichever set of parastichies this may be supposed to belong.

On the other hand, J. E. Loiseau [22] claims to have eliminated a foliar helix in seedlings of *Impatiens roylei*, which have leaves in whorls of three, by pricking one primordium of the youngest whorl to destroy it. In 20 per cent of the seedlings so treated, the number of leaves in each whorl was reduced to two for varying periods after the operation. These results might be due to a reduction of the apical cone, which after the operation was not large enough to give rise to three primordia in a whorl, since in older plants weak normal shoots have only two leaves in a whorl. Microscopic details are needed, but are not given.

However, most theories of leaf determination are based on W. Hofmeister's deservedly famous

rule [23] that each new leaf arises in the largest gap or depression between the existing leaves or other members surrounding the apex. That this is indeed a general rule has since been fully confirmed by many observers and supported by experiments [16, 20, 21, 24]. There do admittedly appear to be some exceptions, for instance in whorl-forming plants after a disturbance [25], but in these some additional factor appears to be at work. The causes underlying Hofmeister's rule have been sought mainly along two rather different lines. In one group of theories it is supposed that the new leaf arises where it does because influences inhibiting or repelling the process of leaf determination spread out both from the summit of the apex and from the centres of the existing leaf-primordia. It is further supposed that the morphological centre of a new leaf is determined first and then the rest of the leaf-base forms around it. In another theory it is supposed that a definite minimum free area of the apical cone at a minimum distance from the summit is needed for the determination of a leaf, and that the necessary free areas become successively available in the depressions between the existing leaves by the continued growth of the whole apical cone. Each leaf is supposed to be determined as a whole over its minimum or primary area. This theory is implicit in the valuable work of G. van Iterson [26] and was supported experimentally and stated in this form by M. and R. Snow [16].

The first of these theories, the repulsion theory, is the more attractive, seeming more physiological and modern, but the writer claims that the second is the one which the experimental evidence supports. It would take too long to argue the case between them at length, and we have done so elsewhere [21]: here only two more recent pieces of evidence will be mentioned. If in *Lupinus albus* and *Euphorbia lathyris* two radial vertical cuts are made in the apical cone so as to confine between them the greater part, but not the whole, of the minimum area presumptive for I_2, the next primordium but one due to rise, then no primordium arises between the cuts and the region between them remains bare, though it grows and remains healthy [27]. Yet if the centres of leaf primordia were determined first, then a centre would be determined between the cuts, and would form an imperfect leaf round itself.

Again, in eleven apices of *Lupinus albus* the central part of P_1, the youngest actual primordium, was removed or destroyed down to its base [27]. After fourteen days the buds were sectioned and the divergence angles measured. The variations of angle were very small in this series, and the primordia I_1, I_2, and I_3 which arose after the operation were all exactly in their normal angular positions (figure 11). Yet I_2 and I_3 were not determined at the time of operation [21], and they made contact at their bases with P_1, the primordium operated upon. There could hardly be a more direct and simple test of the theory that the youngest primordia repel the subsequent ones, and the answer seems quite clear: in *Lupinus albus* at least they do not do so. These results conflict also with Plantefol's opposite hypothesis of leaf induction by existing leaves.

The criticism that the space-filling theory is bare and formal is now partly met by a recent finding that the minimum area for leaf determination is regulated by the summit of the apex. For it now appears that a minimum area must be reached before this area can overcome an inhibition of leaf determination coming from the summit [28].

However, it would be too much to expect this or any other theory to explain completely all the various kinds of phyllotaxis in all species. In some species other causal factors undoubtedly complicate matters. Also, van Iterson's theory does not apply to species in which the leaf-bases are not circular, though the underlying ideas can be extended to them. Neither does it apply, as it stands, to the ferns, in which the bases of the leaves are not in contact. But in this group there are some indications that each leaf-base surrounds itself soon after it has arisen, with a larger, but sharply limited, area unavailable for other leaves [27]. Similar possibilities need to be considered for any regular phyllotaxis systems in other plant groups in which the leaf-bases may be found not to make contact. Such systems seem to be far from common.

OUTLINE OF AN INTERPRETATION OF THE MAIN FACTS OF PHYLLOTAXIS

Armed with a working hypothesis of leaf determination, we can try to interpret some of the main facts of phyllotaxis. At the same time we shall be testing the working hypothesis. The questions will be how the Fibonacci spirals are reached in ontogeny, how it is that the parastichy numbers change repeatedly to higher numbers of the Fibonacci or other summation series to which they belong, and how it is that the divergence angles are so close to the limiting angle for the series. It would take too long to do more than indicate the kind of explanation that is possible.

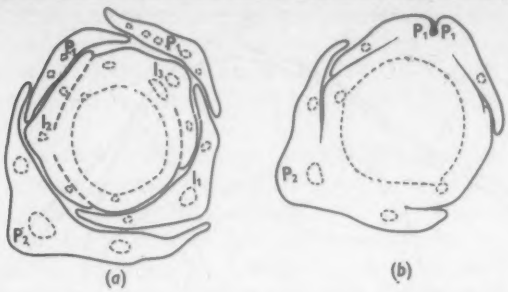

FIGURE 11 – *Transection of apical bud of* Lupinus albus *14 days after removal of the central part of the youngest leaf-primordium,* P_1.

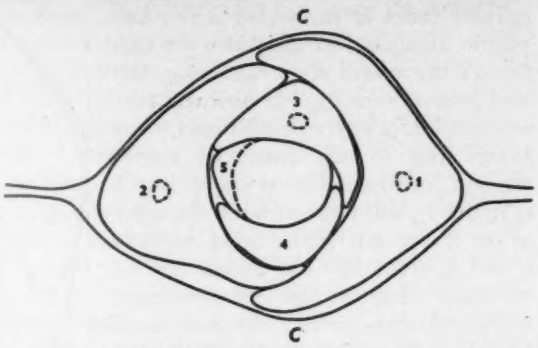

FIGURE 12 – *Apical bud of very young seedling of* Lupinus albus. *The cotyledons are marked* C.

On van Iterson's theory [26] the bases of the young leaves are, apart from special cases, circular when seen from a direction at right angles to the surface in which they are inserted. From these bases the leaves at first grow up vertically, and horizontal sections through their upstanding parts give the familiar crescentic leaf-shapes seen in bud sections. The leaf bases in constant phyllotaxis are considered to form a continually similar system of touching circles. The height of the phyllotaxis, measured by the parastichy or contact numbers, depends on the arc of the circumference covered by each young leaf base. But with some values of these arcs two or more different pairs of numbers, belonging to different summation series, are possible, and the decision between them depends on how the system has developed.

As an example of development we will take the seedling of *Lupinus albus* (figure 12). The opposite cotyledons are followed by two leaves, 1 and 2, in the transverse plane, which are opposite but unequal. Leaf 2 is smaller and inserted higher on the axis than leaf 1, and is therefore younger: it makes contact with leaf 1 on both sides. In order to understand the positions of the leaves, one must remember their circular bases. If each leaf is determined in the first sufficient space that reaches a sufficient distance below the summit, then one may think of its base as if it were a circular plastic disc, partially wrapped round the apical cone and free to slide down the oblique surface under gravity. It is then clear that leaf 2, being wrapped round an arc of more than 180°, must rest symmetrically on the two sides of leaf 1, which also covers more than 180°.

Leaf 3 covers a smaller arc, too small for its base to rest on the two sides of the base of leaf 2. Where, then, is the lowest position for it, the position into which its base may be imagined to sink? Not opposite to leaf 2, since there it would be directly over the median and highest part of the base of leaf 1. Instead, the position which leaf 3 occupies is above one side of leaf 1 and of leaf 2, and rather closer to leaf 1, which is inserted the lower. Thus leaf 3 makes contacts with 1 and 2. Leaf 4 arises above the other sides of leaves 1 and 2, but it cannot arise at the same time as leaf 3, since the nearer side of leaf 3 extends too far round the apex to leave room for another leaf at the same level. So leaf 4 has to wait until it can occupy a slightly higher position rather closer to leaf 2, and with one of its sides above the side of leaf 3. With leaf 4 the spiral sequence has started, and the apex is committed to the Fibonacci series, since leaf 4 makes contacts 1, 2, and 3.

The arcs of the subsequent leaves are not much smaller until just before flowering, and the contacts either continue to be 1, 2, and 3, or more often become 2 and 3 only. The early divergence angles in these young seedlings oscillate, being alternately above and below the Fibonacci angle, to which they gradually approximate. On the same principles, based on space-filling theory, the course of development can be readily explained in many other seedlings, and also in axillary buds and after various operations on stem apices. Indeed, the theory fits so many facts so well that experience in applying it brings increasing confidence.

In many species other than *Lupinus albus* the leaf arcs continue to fall, and the contact numbers to rise up the Fibonacci series. How are these numbers to be explained? Figures 13 and 14 indicate the answer. In figure 13, a transection of a bud of a young shoot of *Sempervivum calcaratum*, it can be seen that the young leaf marked 0, the youngest leaf clearly shown, makes contacts 2 and 3. Let us again imagine, as a model, that the

circular bases of the young leaves are plastic disks able to slip down the surface of the apical cone, and that this bud goes on growing. If now the subsequent leaves cover smaller arcs, then before long in our imaginary model the leaf corresponding in age to leaf 0 of figure 13 will not rest upon the sides of the leaves that would form contacts 2 and 3, since all these leaves will be too small. Instead, the leaf considered will slip down between those that would form contacts 2 and 3, and will be supported instead on those forming contacts 3 and 5 below. This change may have occurred at the next younger leaf, and the change has certainly occurred in figure 14, a transection of a bud of an older shoot of the same species, where the leaves marked 2 and 3 are resting on contacts 3 and 5. Similarly it can be seen in figure 14 that if the leaf arcs were to diminish still further, the corresponding leaves would slip through the gaps between contacts 3 and 5 and rest on contacts 5 and 8, as the leaf marked 1 has actually done. A still further fall of arc would lead to contacts 8 and 13, and so on. The process is indicated by the straight lines drawn outwards from the centres of the youngest leaves in figures 13 and 14.

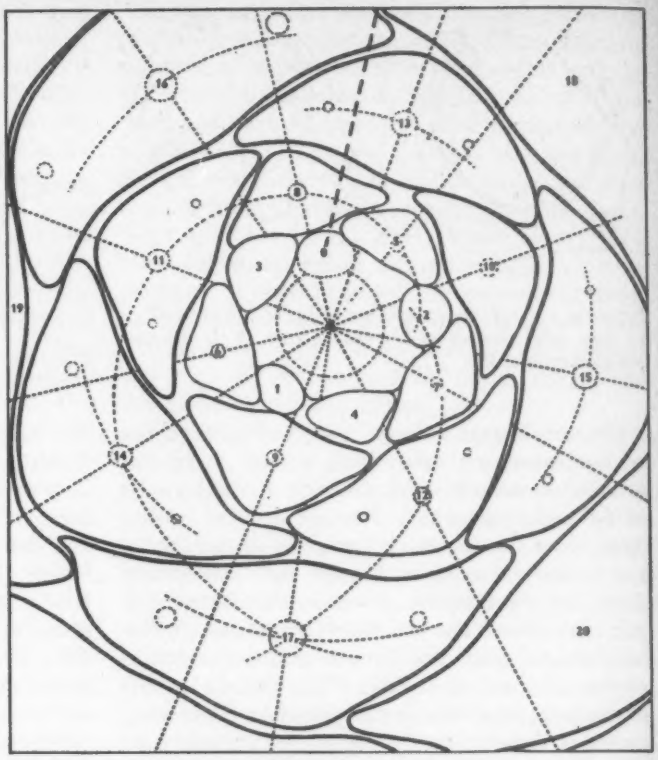

FIGURE 14—*Apical bud of older plant of* Sempervivum calcaratum. (*After Church*, 1920.)

Thus essentially a fall in arc leads from lower to higher contact numbers of the Fibonacci series, because the centres of leaves differing in age by numbers of plastochrons that are successive numbers of the series straddle the same radius, falling alternately on each side of it. This can be verified either on bud sections or in theoretical diagrams, and is discussed geometrically by Richards [5] and several earlier writers. The same holds, indeed, for phyllotaxis systems belonging to any summation series, and an example in another series is indicated by the radius drawn through leaf 0 in figure 8. Thus, whatever the pairs of contacts with which a spiral system starts, the contact numbers will rise up the summation series constructed from the first pair if the leaf arcs diminish sufficiently. The principle underlying this explanation holds good with any theory of determination based on Hofmeister's rule, and Richards [5] has emphasized that as the phyllotaxis rises, the gaps between the leaves become smaller, and so the new leaves will be located more and more accurately. Incidentally, the curious fact may be noted that in buds with threefold contacts the leaves differing in number by successive numbers

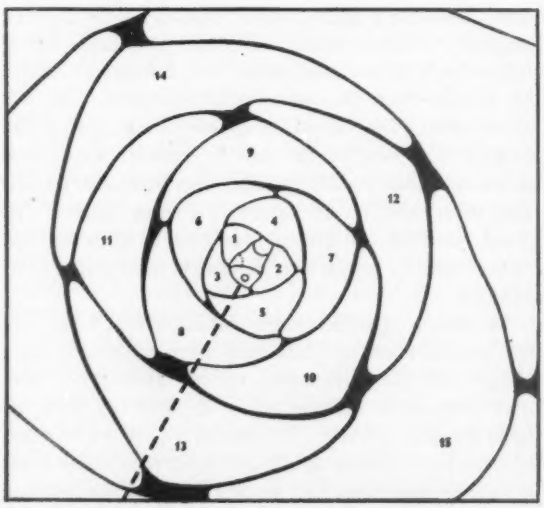

FIGURE 13—*Apical bud of young plant of* Sempervivum calcaratum. (*After Church*, 1901.)

of the summation series concerned are found often, or perhaps always, to straddle a steep curve, instead of a radius. This is indicated by the curved lines drawn outwards from leaf 0 in figures 9 and 10.

The theory of van Iterson comes near to explaining also the mean values of the divergence angles, but here a difficulty remains. He has shown geometrically that if his basic postulates are granted concerning the shapes of the apex and young primordia, then a regular contact system of primordia with any particular pair of contact numbers must have a divergence angle within a certain range. This range always includes the limiting angle for the summation series to which the contact numbers of the system belong, and it is very narrow when these numbers are moderate or high, for instance 3 and 5 or higher numbers in the Fibonacci series, but wider when the contact numbers are low. On this theory, therefore, one would expect the mean divergence angles to be very close to the limiting angle of the series concerned when the phyllotaxis was fairly high but to vary considerably in different species when it was very low.

But the difficulty is that, even in species with the low contacts 1 and 2, the mean divergence angles are commonly close to the limiting Fibonacci angle when the phyllotaxis is fully established, as was pointed out by van Iterson himself, although on his own theory the range possible for them is large—from 128° 34′ to 180°. Similarly in three species with contacts 1 and 2 studied by Fujita [8], the peaks of the frequency distributions of the divergence angles are at 137° or 138°, and are quite sharp. This difficulty was discussed by van Iterson, who suggested a rather difficult explanation. Another possible line of explanation is the following. A wide range of angles is indeed possible with contacts 1 and 2, but, on van Iterson's theory, within this range every different angle is associated with a different leaf arc. If therefore the Fibonacci angle has perhaps some biological advantage, then natural selection may have brought about a close approach to this angle even in species with contacts 1 and 2, by selecting and fixing genetically the corresponding leaf arc.

Among other problems remaining to be studied are the causes of the stability of phyllotaxis systems when accidentally disturbed, the developments leading to contact numbers belonging to other summation series, and above all the nature of the process by which, on the theory here adopted, each successive available space on the apical cone organizes itself to form a leaf. There are also still several plant groups with special and interesting kinds of phyllotaxis which deserve to be studied specially.

ACKNOWLEDGMENTS

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Germanium and its uses

J. N. ALDINGTON and H. W. CUMMING

In a recent issue of ENDEAVOUR (13, 101, 1954) K. K. Darrow described the theory of semiconductors and their significance in the physics of the solid state. In the practical application of semiconductors, germanium, an element about which very little was known even fifteen years ago, occupies a place of unique importance. Its preparation on a considerable scale, in the form of virtually pure single crystals, presents many points of interest. Germanium is also finding a further important use as a deep-red phosphor for lamps.

Fifteen years ago, in spite of its wide distribution in the Earth's crust, the element germanium was unfamiliar even to the scientific world and quite unknown to the general public. Today, notwithstanding the difficulties associated with its extraction and purification, it is one of the most important of the rarer elements.

Three developments have lead to this change. The first was the production of a germanium rectifier capable of withstanding high back-voltages; the second was the pioneer research at Bell Telephone Laboratories which lead to the development of a germanium triode, or transistor, capable of amplifying; and the third was the production of germanium compounds which fluoresced in the deep-red region of the spectrum. As a result of these discoveries, and many others stemming from them, interest in germanium has been greatly stimulated: many groups of research workers are studying solid-state physics, and much literature on the subject has been published.

Historically, the discovery of germanium was of considerable scientific interest. In 1871, Mendeléef predicted the existence of a further metal in Group IV; he gave it the name eka-silicon and detailed its principal properties. In 1886 Winkler discovered germanium in the rare mineral argyrodite—a mixed silver-germanium sulphide containing some 7 per cent by weight of germanium—and it was found to have the properties of the element whose existence Mendeléef had predicted.

No massive source of germanium has so far been discovered, even though, in association with other minerals, germanium-containing compounds are present in the Earth's crust to the extent of about one part in 150,000. The major source of the element in Great Britain is flue dust from gas works. Certain British coals contain germanium compounds in small concentrations, and it has been found that it is present to the extent of about 1 per cent by weight in the dust from retorts making producer gas. The method of extraction from the flue dust consists essentially in concentrating the germanium as a copper-iron-germanium alloy and then removing it in the form of its tetrachloride. After purification by fractional distillation, the germanium tetrachloride is decomposed by water, and the resulting dioxide is finally reduced in hydrogen to the metal [1]. The more important physical properties of the element relevant to the present discussions are shown in table I.

Apart from its uses as a red-fluorescing phosphor and as a semiconductor, germanium finds minor applications in dentistry and in the production of glasses capable of transmitting infra-red radiation.

TABLE I

Principal physical properties of germanium

Atomic weight	72·6
Electronic structure	2 8 18 4
Melting-point	959° C
Relative density	5·47
Electrical resistivity (intrinsic)	60 ohm cm
Electron mobility	3600 cm^2/volt sec

GERMANIUM-CONTAINING PHOSPHORS

The high-pressure mercury electric discharge lamp, as opposed to the familiar fluorescent lamp, which has a low-pressure discharge, has become of considerable importance as a light source during the twenty-five years which have elapsed since its development. The disadvantage of its dominant yellow-green radiation has, however, adversely affected its application in circumstances where reasonable colour discrimination is desirable or necessary. Methods for efficiently adding blue and, even more important, red light to the primary mercury radiation have always been regarded as important objectives of research on lamps. Many methods have been tried and some have been adopted, with varying success. A particularly important possibility, recognized even in

the days of the Cooper-Hewitt lamp, was that of converting some of the ultra-violet radiation into red light by fluorescence. The organic dye rhodamine and some of its derivatives were used for this purpose, but while initially successful they gradually bleached under the ultra-violet irradiation. Lamps containing inorganic sulphide phosphors having red-fluorescing properties have been used for many years; the general method is to coat with the phosphor the inside of an outer bulb containing the mercury lamp. While a useful effect can be obtained, the amount of red light which can be added in this way is far too small to correct fully the deficiencies of the mercury radiation. It is also necessary to use a fairly large outer bulb to carry the phosphor, because the efficiency of the sulphide phosphors rapidly declines at temperatures above about 120° C.

There was thus an urgent need for a phosphor capable of efficient operation at temperatures of several hundred degrees centigrade and notably effective in converting mercury radiation of 2537 Å and 3650 Å wavelength into deep-red light. From the hundreds of possible compounds that were investigated, a magnesium germanate was eventually developed which had the required properties [2]. This germanium compound is now being produced commercially in substantial quantities, and constitutes a new use for the element. Table II compares the spectral distribution of the light from a plain mercury lamp with that from a lamp of the same type but having the colour modulated by a magnesium germanate phosphor; for comparison purposes figures are also given for a typical daylight from a zenith blue sky having an equivalent colour temperature of 13 700° K. The increased radiation is particularly marked in bands 7 and 8; a small increase in the luminosity of these two bands has a marked effect upon the colour-rendering characteristics of the total radiation.

TABLE II

Percentage spectral luminosities for a plain mercury lamp, for a colour-corrected mercury lamp, and for a typical cold daylight

Waveband (Ångströms)	*Percentage luminosity*		
	Plain mercury	*Colour-corrected*	*Daylight*
1. 3800–4200	0·026	0·022	0·052
2. 4200–4400	0·67	0·54	0·38
3. 4400–4600	0·06	0·10	1·265
4. 4600–5100	0·72	0·96	13·85
5. 5100–5600	53	46·5	44·8
6. 5600–6100	44·4	46·5	31·8
7. 6100–6600	1·0	5·0	7·4
8. 6600–7600	0·13	0·43	0·45

A more subtle application of a similar germanium compound is as an addition to the fluorescent powder normally used in low-pressure fluorescent tubes. In this type of lamp the discharge occurs in mercury vapour at a very low pressure and the primary radiation is emitted principally at the resonance wavelengths of 1850 Å and 2537 Å. The actual source of visible light is therefore predominantly the fluorescent powder which is coated along the whole of the inner surface of the glass tube in which the discharge takes place. The phosphor most commonly employed today, on account of its stability and high efficiency, consists mainly of a calcium halo-phosphate. Antimony and manganese are present as activators, and by varying the ratio of these two elements in the phosphor the colour of the light emitted can be varied from blue to orange; by suitable choice of the proportion of the activators white light can be produced. The quality of this light has proved acceptable for all commercial applications, and a range of near-white colours is obtainable. In spite of this, research workers in Britain and other European countries and in America have long sought a phosphor capable of producing a higher proportion of deep-red light than has so far proved possible with phosphors of the calcium halo-phosphate group. It has been found that a manganese-activated magnesium germanate has the required properties, and that its addition to suitable calcium halo-phosphates, to the extent of some 10 per cent by weight, permits appreciably better colour-rendering of some of the more difficult hues. Not only is the deep-red colour-rendering of the fluorescent lamp improved, but there is a noticeable reduction in the effect of the 4047 Å and 4358 Å mercury lines, which, although of low intensity, have a high chromatic effect. There are therefore considerable possibilities for germanium phosphors in the further development of fluorescent tubes.

GERMANIUM AS A SEMICONDUCTOR

Since the development at Purdue University, some fifteen years ago, of a germanium rectifier having improved properties, and the announcement by Bell Telephone Laboratories in 1948 of an amplifying device employing a single crystal of

germanium, progress in the development of germanium devices has been rapid and entirely new fields of research in the physics of the solid state are being explored. These developments may directly or indirectly affect the whole future of telecommunications, to mention only one important field. For this reason an understanding of the basic principles underlying the production of semiconductor devices is of general interest. The physical properties and characteristics of semiconductors have been discussed recently in this journal [3] and elsewhere [4]. While it should be appreciated that other materials are receiving attention—particularly silicon and the intermetallic compounds of Groups III and V of the Periodic Table—it is nevertheless germanium which has stimulated the greatest interest and which is almost exclusively the material used in the devices available at the present time.

Types of semiconductor devices already developed include polycrystalline, high back-voltage, point-contact rectifiers; monocrystalline junction rectifiers or diodes; single-crystal triodes (for which the term transistor has been coined); single-crystal tetrodes; phototransistors whose electrical resistivity changes with variation in the incident illumination; and power rectifiers capable of handling currents of hundreds of amperes. This short, and by no means exhaustive, list of semiconductor devices indicates the rapid progress already achieved in this comparatively new field. This progress has been made possible by the concentrated effort of many research laboratories following the important possibilities opened up by the pioneer work in the Bell Telephone Laboratories.

THE TRANSISTOR

The name transistor has been given to a semiconductor device carrying three external electrodes —base, collector, and emitter. Although not strictly analogous, these electrodes may under certain conditions be considered to be roughly equivalent to the cathode, anode, and grid in a thermionic valve. The application of a voltage between base and collector causes a low current to pass, and a change of current between emitter and base produces a proportionately greater change in the current through the collector.

A typical transistor dissipates some hundreds of milliwatts at currents of a few milliamperes. It is an extremely small device in both size and weight, and yet it is robust; there are indications that it may have an almost infinitely long life. Unlike the conventional amplifying valve, the auxiliary power consumption is remarkably small. Crystal devices are potentially suitable for the replacement of all types of valves. Particularly in the fields of guided missiles, telecommunications, electronic computors, and electronics generally, semiconductors are playing an increasingly vital part.

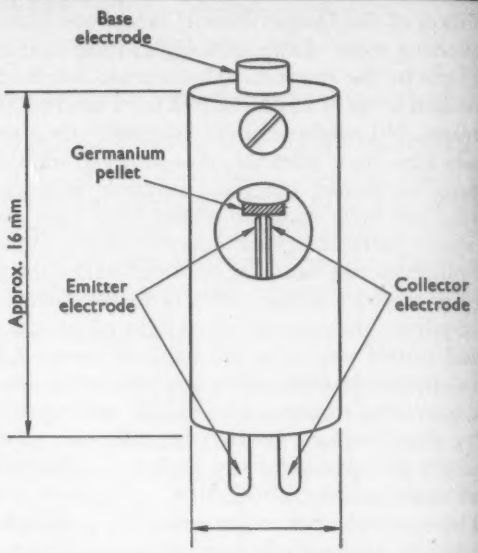

FIGURE 1 – *Diagram of point-contact transistor.*

Transistors are of two main types, commonly termed point-contact [4] and junction. Within the latter group there are three principal divisions, namely grown junction [4], fused junction [5], and surface barrier [6]. It is with the earlier type, the point-contact transistor, that the following description deals. It consists essentially of a base of single-crystal germanium on the surface of which are placed, very close together, pointed wires of phosphor bronze and copper-beryllium; these form respectively emitter and collector. The system may be assembled for convenience in the form shown in figure 1. Further constructional details will be given later in the section dealing with transistor assembly.

PREPARATION OF GERMANIUM SINGLE CRYSTALS

Very pure germanium dioxide is first prepared by ordinary chemical methods [1]; the arsenic content in particular must be reduced to less than 0·05 part per million. The germanium dioxide, contained in special graphite boats, is then reduced in hydrogen to the metal. When reduction is complete, the germanium is fused into an ingot some $9 \times 1{\cdot}5 \times 0{\cdot}75$ cm.

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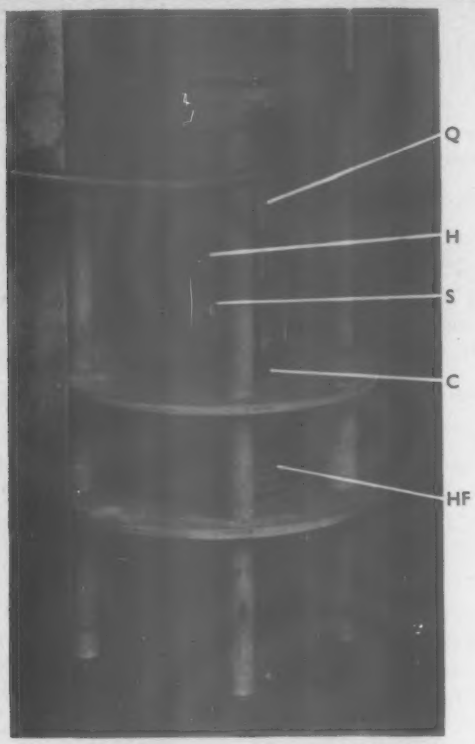

FIGURE 2 – *Apparatus for growing large single crystals of germanium.*

FIGURE 3 – *A large single crystal of germanium.* (× 2)

Further purification of the metal is carried out by a process called zone refining. In this process the carbon boat containing the ingot is drawn at the rate of some 3 inches per hour through a transparent quartz tube filled with nitrogen. During its passage it traverses a laminar high-frequency electric field which is at right-angles to the direction of travel of the boat. At any instant, therefore, only a thin section of the germanium ingot is heated to the melting-point, and passage of the ingot through the heated zone causes a liquid phase, in the form of a wafer, to pass from one end of it to the other. It has been found that this liquid phase carries to the trailing end of the ingot the bulk of the residual impurities, and repeated passage of the ingot through the field results in a very high final purity. Three high-frequency zones are formed in series in the authors' apparatus. With good initial material three passages of the boat through the furnace generally produce an ingot having the required degree of purity; this is determined by measurements of electrical resistivity of the ingot at different points along its length. The result of a typical test on a bar of refined germanium is shown in figure 4. It will be seen that some three-quarters of the ingot has a resistivity of the order of 50 ohm cm, indicating the attainment of the required degree of purity. The less pure part of the bar, defined by its low resistivity, is rejected, the purer portion being used for the next stage to produce single crystal material. Here the technique employed is similar to that used for the production of large crystals of many other elements and compounds. In essence, a seed crystal is partially immersed in liquid germanium maintained at or near the melting-point. The crystal is grown by gradually withdrawing the seed from the melt, the whole operation being carried out in an inert atmosphere. Figure 2 shows apparatus for this purpose developed in the authors' laboratories. A suitable charge of the purified metal, together with a predetermined addition of germanium-antimony alloy, is loaded into the carbon crucible C supported inside a quartz cylinder Q, within which an atmosphere of nitrogen is maintained. A seed crystal S, having the desired orientation, is clamped in the holder H, which can be rotated continuously and raised or lowered. The temperature of the molten charge is then adjusted to just above the melting-point of

vitamins that have to be provided. The power to synthesize these vitamins is developed later, although some organs, notably roots, may never acquire it, and always need a constant supply from the aerial parts of the plant.

But these known co-factors are not the only growth substances provided from the surrounding tissues. Excised embryos may still fail to grow on culture media containing all the vitamins known to be essential, although they may succeed if supplied with extracts of endosperm tissue. An ideal source of the unknown factors has been found to be coconut milk, which is virtually liquid endosperm. There are indications that at least two substances may be present, one controlling cell proliferation and another acting as a co-ordinating factor in organ development. Some of these factors have been isolated, but their chemical constitutions are not known in detail.

Many problems of seedling growth still remain to be explored. There is the mystery of why seed leaves (cotyledons) grow to such a huge size compared with the embryonic root and shoot: a growth co-ordinating substance is most probably involved. Why the embryo, when it has reached a certain limiting size, should stop growing and enter into a state of dormancy is still not understood. Only in a very few plants, e.g. the mangrove tree of tropical estuaries, does the embryo continue to grow, and the seed germinate, on the plant without a resting period. This stoppage of embryo growth is presumably imposed by the accumulation of an inhibitor. There is no doubt that the seed coats and the flesh of many fruits contain chemicals which prevent the subsequent germination of the mature seed [4]. The presence of such inhibitors in the fruit flesh probably delays seed germination until the fruit has been dispersed from the plant and the seeds liberated from it. The seed-coat inhibitors may simply be leached out by rain or they may need special external conditions for their destruction. For example, some seeds are stimulated to germinate by light (e.g. lettuce), and this can be explained by a photo-inactivation of the inhibitors of the seed coat. Many natural germination inhibitors are unsaturated lactones.

But this non-growing period of the embryo is not necessarily one of inactivity, since many fundamental changes may be taking place. Many seeds, for example, need a period of dormancy, under particular environmental conditions varying with the species (e.g. low temperatures in apple), before they will germinate. This may be associated with the destruction of a germination inhibitor or with 'maturation' changes in the cells of the embryo. These changes may determine in large part the subsequent developmental behaviour of the growing plant. Thus if sown in the spring the seeds of winter varieties of temperate cereals will not flower and set seed in that season. Such seeds need a certain minimum period of exposure to a temperature near freezing point, to produce a condition in the embryo favourable to rapid flowering when the plant eventually grows. This process of 'vernalization,' as it is called, can be reversed by subsequent exposure to a high temperature [5], provided it is applied within a certain limited period. The most probable explanation of this phenomenon is that the temperature treatments are affecting the level of a flower-promoting hormone, or its precursor, in the embryo, low temperatures favouring its accumulation and high temperatures its destruction. This putative flowering promoter has not yet been isolated, but has been named 'vernalin' [6].

THE SEEDLING

When the seed is mature and external conditions of light, temperature, and water supply are optimal, it will germinate. This involves the resumption of biochemical activity, in which reserve carbohydrates and proteins are hydrolysed and the mobile products translocated to the embryo for growth synthesis. Root and shoot commence to elongate and push their respective ways out through the seed coat into the substrate. This elongation is under the control of that group of plant growth substances known as the auxins, of which β-indolylacetic acid is the most important, perhaps the only, natural representative. It is produced by the apical growing points, where cell division is actively going on. It is generally held to be produced, by oxidative deamination and decarboxylation, from the amino acid tryptophan, which is mobilized from reserve proteins in the seed. This has not been firmly established, however, although the very close association of β-indolylacetic acid production with organs showing active protein synthesis suggests that it is a by-product of that process, perhaps being synthesized, at the same time as tryptophan, from a common precursor. Many other indole compounds which induce auxin responses when applied externally to test organs of plants have recently been identified in plant extracts. They include β-indolylacetonitrile, β-indolylacetaldehyde, and β-indolylpyruvic acid. The last two may be intermediates in β-indolylacetic acid metabolism. β-indolylacetonitrile and

FIGURE 1 – *Flower formation in Cabezona pineapple 7 weeks after treating a plant 24 months old with 10 p.p.m. α-naphthylacetic acid. (By courtesy of Dr J. van Overbeek)*

FIGURE 2 – *Selective weedkiller used for the control of charlock in oats. 2,4-D was applied to the top right-hand plot in May: the photograph was taken in July. The lower plot was untreated.*

β-indolylacetaldehyde have probably no auxin activity themselves, but are rapidly converted to β-indolylacetic acid by enzymes in extending cells. The nitrile may have an important role to play as an inactive reserve of auxin potential. Auxin metabolism has been reviewed by S. A. Gordon [7].

Although the control of shoot extension by auxins is well established, the situation in roots is more obscure. Root extension is prevented by concentrations of applied auxin which promote shoot growth. On the other hand, very low concentrations (1 part in 10^{11}), which stimulate root growth, have no effect on shoots. The position is further complicated by the fact that homologues of β-indolylacetic acid, which antagonize its actions in shoots and roots, may themselves promote root growth in very low concentrations. Whether there is in roots 'No growth without auxin', as postulated by F. W. Went [8] and held to be true for shoots by the majority of plant physiologists, is still a matter for discussion.

There are many synthetic compounds, similar in chemical structure to β-indolylacetic acid, which are extremely active as auxins. They differ

FIGURE 3 – *Antigeotropic effects with rape seedlings (top) and ryegrass (bottom), showing controls (left) and the influence of an active compound (right).* (J. Sci. Food Agric., 5, 32, 1954.)

FIGURE 4 – *Sections of tomatoes, showing fruit structure. Centre: Normal seeded tomatoes. Left: Tomatoes set with α-naphthylacetic acid. Fruit of high quality with fully developed pulp, but no seeds. Right: Tomatoes set with 2,4-dichlorophenoxyacetic acid. Fruit of poor quality, with poorly developed pulp and puffy flesh. (By courtesy of the Director, Long Ashton Research Station.)*

FIGURE 5 – *Promotion of flowering in bean by treatment with 2,3,5-tri-iodobenzoic acid (T.I.B.A.). Left: Control (apical bud removed by hand, since it is destroyed by T.I.B.A.). Right: Watered daily with T.I.B.A. (40 ml of a 50 p.p.m. solution). (By courtesy of Dr C. J. Gorter, Laboratory of Horticulture, State Agricultural University, Wageningen, Holland.)*

FIGURE 6 – *Isopropylphenyl carbamate used for the prevention of sprouting in potatoes, stored for 226 days. Left: Control, untreated. Right: Treated at the start of the storage period with I.P.P.C.*

from natural auxins in that they are highly toxic to plants if applied even in slight excess. Furthermore, the low threshold concentration at which this toxicity sets in varies widely from species to species of plant, thus allowing the use of these compounds as extremely efficient selective weedkillers. Two such compounds that are now used extensively all over the world are 2,4-dichlorophenoxyacetic acid (2, 4-D) and 2-methyl,4-chlorophenoxyacetic acid (figure 2).

The young seedling, in establishing itself, responds with great sensitivity to the stimuli of light and gravity. The developing root system grows in such directions as to explore the maximum soil volume, and the shoot disposes itself to receive optimal illumination for carbon assimilation. There is no doubt that in these responses auxins play a central role. Thus unequal illumination of sensitive organs leads to spatial differences in auxin concentration. The resulting differential growth brings about curvatures in the organ concerned and re-orientation towards the source of the light. The underlying cause of this redistribution of auxin is still only partially understood. There is strong evidence that β-indolylacetic acid undergoes a photo-oxidation in which riboflavin acts as the sensitizer, but the complexity of response to different light intensities shows that this cannot be the only factor concerned. The geotropic response has also been attributed to a redistribution of auxin. There is direct evidence that auxin does accumulate on the lower side of horizontally disposed shoots, thus stimulating the growth of the lower half and causing a re-orientation of the shoot into the vertical position. In horizontally placed roots, the same accumulation on the lower side is supposed to inhibit growth there and hence cause a downward trend. The experimental evidence for this is much less convincing, especially in view of the uncertain role of auxins in root growth. In some organs, e.g. underground stems that grow horizontally and at a constant level below the soil surface, the distribution of at least two different hormones may be involved in maintaining this adjustment [9, 10].

Recently compounds have been discovered which disturb the mechanism of root response to gravity, presumably by interfering with the natural hormone system (figure 3). The use of such compounds may prevent the establishment of the roots of weed seedlings and thus provide a new approach to weed control [11].

Growth factors other than auxins seem to play a part in the growth of leaves. Darkness causes seedlings to grow tall and spindly, a response usually attributed to their higher auxin content, while the same environmental conditions prevent the expansion of leaves. The growth of leaf blades has been shown to be promoted by the organic base adenine, an essential component of the nuclear proteins and of many important coenzymes associated with the supply of metabolic energy. Other unknown factors are undoubtedly involved. The extension of leaf veins, however, is apparently promoted by auxins. It is not surprising, therefore, that the application of synthetic auxins, which are not metabolized to any extent by plant tissues, can alter the balance of growth factor requirements and bring about dramatic changes in leaf form. Indeed, such active and stable auxins as 2,4-dichlorophenoxyacetic acid can markedly inhibit blade expansion and cause a wide variety of deformities.

THE DEVELOPING PLANT

As the plant increases in size new organs come into being, and the form characteristic of the adult is assumed. In the above-ground parts of many plants this will be largely a result of the number and position of the lateral branches arising from the buds situated in the leaf axils. The early growth, and hence subsequent development, of these lateral buds is suppressed by the terminal bud of the main shoot or branch. The kind of development which ensues will depend largely on the behaviour and fate of this terminal bud. This phenomenon of apical dominance plays a major role in determining the shape of most plants. Auxin produced by the apical bud has long been claimed by many as the mediator of this correlation phenomenon, being translocated from this centre of production to the laterals, which are then inhibited. Other workers have postulated a special inhibitor whose production is associated with auxin levels. Non-auxin growth inhibitors showing some of the physiological properties of this theoretical substance have recently been extracted from plants, but they have not yet been identified. Again the story is not as simple as this would suggest. For example, when a solution of the synthetic growth inhibitor, maleic hydrazide, is sprayed on plants, it may remove apical dominance and allow laterals to grow out. This suggests that there is a real difference in the sensitivity of different buds to growth substances, and this may contribute considerably to correlative behaviour. But we should not be too prone to attribute every growth phenomenon solely to hormone action.

Work under F. G. Gregory [12] has shown conclusively that, in flax at least, competition for a nutrient (nitrogen) may play an over-riding part in determining apical dominance. Both synthetic auxins (e.g. the methyl ester of α-naphthylacetic acid) and growth inhibitors, such as maleic hydrazide and *iso*propylphenyl carbamate, are being used for the suppression of bud growth (sprouting) in stored vegetables (e.g. potato, carrot, onion), thus preventing the wastage that could otherwise occur in the later stages of storage (figure 6).

The formation of lateral roots is undoubtedly affected by auxins, since it can be greatly promoted by external applications of these substances. A very important practical application of this phenomenon is in the promotion of root formation in plant propagation by cuttings. Much indirect evidence exists for the participation of other factors in natural root genesis. One is a hypothetical 'rhizocaline' provided from shoots. In view of the complex vitamin requirements shown by excised roots growing on artificial media containing sugars it is not impossible that this 'rhizocaline' may be a vitamin. Since lateral roots are always produced in a special internal tissue layer, a third rooting factor, strictly confined to these cells, has been postulated.

In perennial woody plants growth in girth of stems takes place by the activity of a sheath of special cells (cambium) situated between wood and bark. This growth activity is highest in the spring and declines as summer advances, and accounts for the formation of annual rings in trees growing in temperate climates. This rhythm is exactly correlated with auxin production by the young buds in the spring, a wave of auxin from the buds flowing down the cambial sheath of cells and initiating and promoting its growth activity. Again other factors are involved, since these cells will not react to applied auxins in the winter when in a dormant condition. Dormancy has first to be broken (e.g. by treatment with ethylene) before the cells can respond. The same cells are responsible for the production of tissue (callus) to cover wounds in trees. From time to time special wound hormones (e.g. traumatic acid, $COOH.CH{:}CH.(CH_2)_8.COOH$) produced by the damaged cells have been claimed as the determining factors of wound response.

Whereas in most perennial woody plants branches persist and grow for the whole life of the plant, leaves reach maturity at an early stage and show no further growth. After a season or so of active synthesis, they are shed and are replaced. Leaf fall is brought about by the loosening of the cells in a special cell layer (abscission layer) at the base of the leaf stalk. The strength of the stalk in that region is thereby lost and the leaf is then readily removed by any mechanical disturbance, such as wind. Abscission takes place when the leaf has become senescent and its synthetic powers have failed; its direct cause is the declining supply of auxin from the blade. Auxin presumably acts, either directly or indirectly, by inhibiting the enzymes responsible for the biochemical changes causing the loosening of cells of the abscission layer from one another.

REPRODUCTION

In higher plants the switch to the reproductive state, when some of the growing points change the course of their development to produce flower primordia instead of leaf primordia, is determined very largely by the onset of particular day-lengths and by previous temperature conditions. The associated phenomena are too extensive and complicated for any general statement in an article such as this, but there is very compelling evidence that a flowering hormone is involved [13]. Day-length discrimination is carried out by the leaves, which, under optimal lengths of day and night, originate some kind of influence which passes thence to the growing-points and induces the change-over from the vegetative to the flowering state. This influence will pass a graft union, suggesting that it is a chemical substance. On the other hand, it will not diffuse across a water gap between two such graft partners, and this suggests that simple diffusible substances are not involved. So far, the insuperable obstacle to the acceptance of the existence of flowering hormones has been that, despite many and repeated attempts, no extract from a flowering plant has yet caused flowering when applied to vegetative plants.

It is natural that auxins, active in so many growth processes in plants, should have been thought of in connection with flowering. Undoubtedly they do affect flowering behaviour, but their true role in flower induction is still very obscure. Many now believe that auxin, although not itself a flowering hormone, must be present at an optimal level if flowering is to take place. The situation is by no means clear, however, since some plants (e.g. pineapple) can be induced to flower by auxin (α-naphthylacetic acid) application (figure 1), while in others flowering is greatly promoted by the application of substances which are regarded as antagonists of auxin action (e.g.

2,3,5-tri-iodobenzoic acid in the bean (figure 5)). Direct indications from assays of natural auxins during flower induction and development show marked changes in free auxin concentrations, but there is no consistent picture. The effect of synthetic auxins on flowering has been fully exploited in the pineapple industry, where the date of fruiting can be precisely determined by carefully timed sprays of very dilute α-naphthylacetic acid solutions. This completely obviates the difficulties of harvesting and marketing previously resulting from the normal random spread of fruiting.

When a flower is fully developed and conditions are suitable, it is pollinated. Pollen grains germinate on the receptive part of the female organ (stigma) and pollen tubes penetrate to the ovules, where the nuclear fusion mentioned earlier takes place. The pollen brings with it not only male nuclei for fertilization but also a supply of β-indolylacetic acid which triggers off the growth processes of the young fruit. If this auxin stimulus is not received, then an abscission layer forms across the base of the flower stalk and the unfertilized flower is shed. Once the growth of the young fruit and its contained seed has started, there is a continued production of auxin which prevents this layer forming and also maintains the growth of the fruit tissue. In some fruit, particularly seedless varieties, sufficient auxin is produced in the fruit tissue itself, but in most plants the young embryo and the endosperm are the sources of this hormone for fruit growth. Recent work under L. C. Luckwill has demonstrated waves of auxin production during fruit development in both apple [14] and blackcurrant [15]. At least three hormones may be involved. The well known shedding of small immature fruit (June drop) and the ultimate fall at maturity are both closely correlated with low levels of auxin at these two stages in the life of the fruit. As the fruit grows there gradually accumulates in the flesh the germination inhibitor described at the beginning of this article.

Synthetic auxins have two very important applications in fruit growing. Under conditions unfavourable for pollination dilute solutions can be sprayed on flowers to induce the setting of the fruit and subsequent production of a full crop, which will of course be largely seedless. This has its greatest application in commercial tomato growing (figure 4), and is being extended to other fruits such as figs and grapes. Synthetic auxin sprays can also be used to retard the abscission and fall of maturing fruit, such as apple, thereby reducing damage and loss and also allowing greater flexibility in the planning of harvesting operations. An incidental advantage is that the post-harvest ripening and quality of the fruit may be improved. At all stages in the growth and development of plant organs specific growth substances seem to be in control. So far research has been dominated by studies on the auxins, in particular β-indolylacetic acid, but with the application of paper chromatography to the study of plant growth substance, and the development and refinement of assay methods, we look forward to the isolation in the not too distant future of other postulated substances that have so far eluded identification.

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The history of the marine chronometer

SIR HAROLD SPENCER JONES

The accurate determination of position at sea now presents so few problems, unless weather conditions are so adverse as altogether to preclude astronomical observation, that it is perhaps difficult to appreciate the very grave difficulties it presented to navigators less than two hundred years ago. As the precise determination of longitude depends directly upon the availability of an accurate timepiece, the marine chronometer, the development of which is traced in this article, is a navigational instrument of absolutely fundamental importance.

The problem of finding the longitude of a ship at sea for long defied solution. The longitude difference between two places is equal to the difference between the local times of the two places at the same instant. The determination of local time by a ship at sea presents no difficulty; the determination of its longitude relative to some standard meridian therefore depends upon knowing the time on that meridian. If the ship can be provided with an accurate timepiece, set to the time on the standard meridian, the problem is solved.

The use of a timepiece for determining longitude at sea was first proposed in 1530 by Gemma Frisius, in his *De Principiis Astronomiae et Cosmographiae*. But the timekeeping of the clumsy watches of his day was far too erratic to be of any value. The first attempt to design and construct a timepiece that would keep time at sea was made by Huygens in 1660. His marine clock was controlled by a half-seconds pendulum; when tried at sea it proved to be hopelessly erratic, as the slightest motion of the ship upset the pendulum. He then replaced the pendulum by a balance and balance spring, but the lack of a method of compensating for changes of temperature, and various other defects, resulted in poor timekeeping.

The next attempt of importance was made by Henry Sully (1680–1728), a former apprentice of George Graham, the leading English horologist. Newton and Wren turned Sully's attention to the problem of constructing a clock for use at sea. He made several marine timepieces, one of which is in the Museum of the Clockmakers Company in the Guildhall, London. An oscillating horizontal bar, connected with the balance by a silk cord working between cycloidal cheeks, replaced Huygens's pendulum. The escapement, of his own design, had some merits, and friction rollers were used for the first time to minimize friction at the pivots. Trials made in sheltered waters in 1726 were promising, but those on the open sea were a failure. The oscillating bar was a horizontal pendulum and was influenced by the accelerations produced by the pitching and rolling of the ship. Sully designed also a marine watch, which he mounted in gimbals; it had some promising features and might have been developed into a satisfactory timekeeper, but his comparatively early death put an end to his experiments.

A solution to the problem of determining the longitude at sea had become so urgently needed that in 1714 the British Government offered an award of £10,000 for any method capable of determining a ship's longitude within one degree, of £15,000 if within 40 minutes, and of £20,000 if within 30 minutes. A permanent body of Commissioners, known as the Board of Longitude, was appointed to adjudicate on applications for the award; they were empowered to pay one half of the award when the majority of the Board was satisfied that the method was practicable and useful, the other half when a vessel using the method had sailed to a port in the West Indies without erring in her longitude by more than the specified amount.

Many quite impracticable schemes were submitted to the Board. It was not until 1764 that all the conditions for the award were successfully met, by a timepiece constructed by a Yorkshire carpenter and mechanic, John Harrison (1693–1776); owing to conditions imposed by the Board, however, payment of the award in full was not made until 1772. In 1728 Harrison took to London the drawings of a marine clock he had designed, in the hope of obtaining assistance from the Board of Longitude for its construction. On Halley's advice he showed his drawings to Graham, who discerned their promise and lent him £200 without security or interest to enable him to carry on with the construction.

In 1735 Harrison completed his first marine

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FIGURE 1 – *John Harrison (from a mezzotint by Tassaert, published in 1768, after a painting by King). His machine No. 3 is behind, and No. 4 is on the table.*

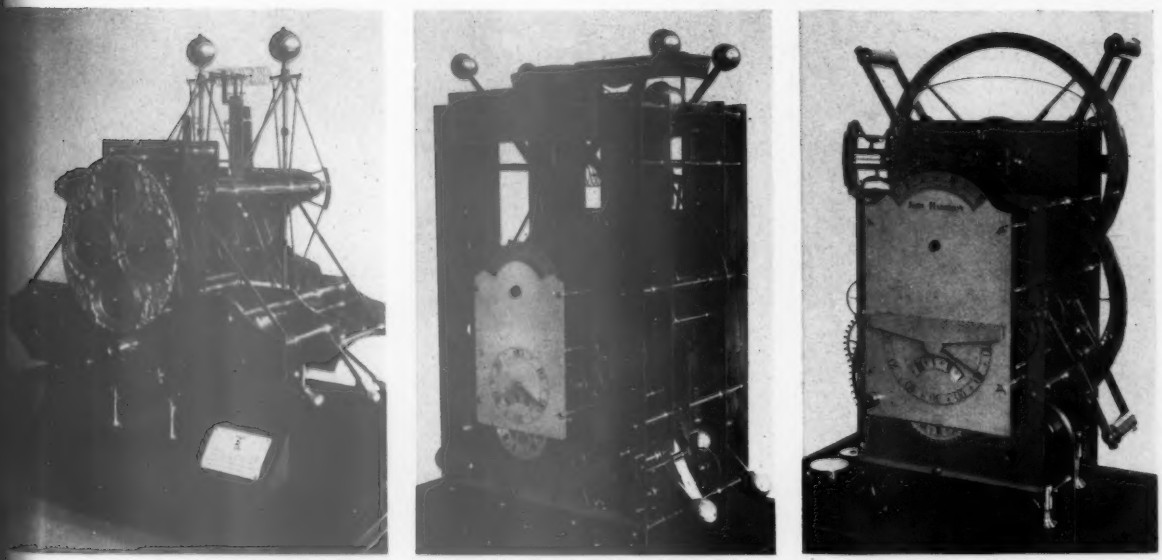
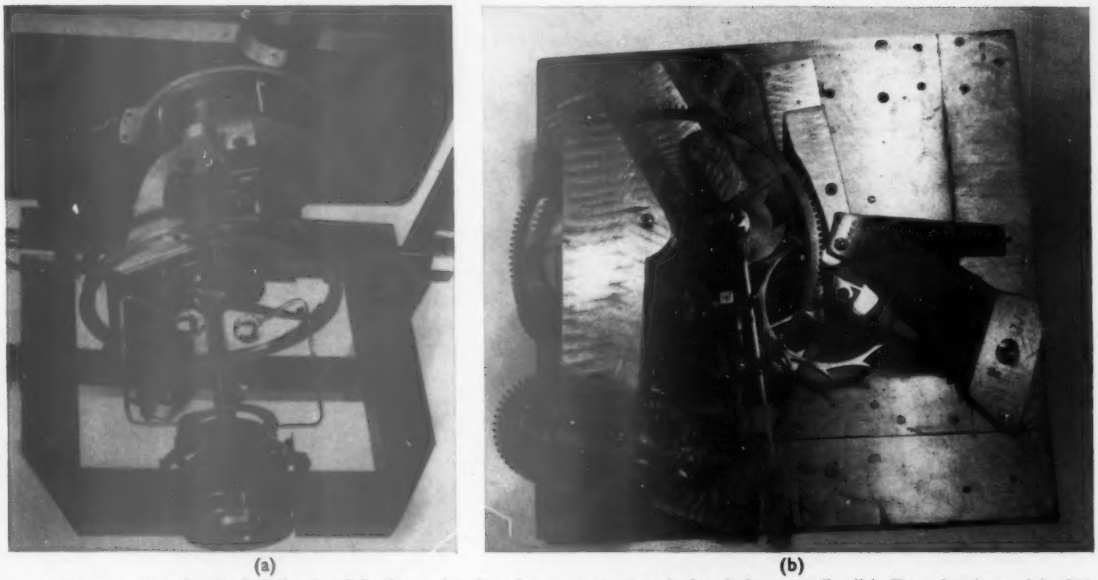


FIGURE 2 – *From left to right: Harrison No. 1, Harrison No. 2, Harrison No. 3.* (*Crown copyright.*)

FIGURE 3 – *Harrison No. 4. Front view and movement.* (*Crown copyright.*)
(*Figures 2 and 3 are reproduced from the originals in the National Maritime Museum, by permission of the Admiralty.*)

FIGURE 4 – *The back plates of Harrison No. 4 and of Larcum Kendall No. 1.*



(a) (b)

FIGURE 5 – (a) *Le Roy's* Montre Marine, *showing thermometers attached to balance staff.* (b) *Earnshaw's model of his spring-detent escapement, made for the Board of Longitude in* 1804.

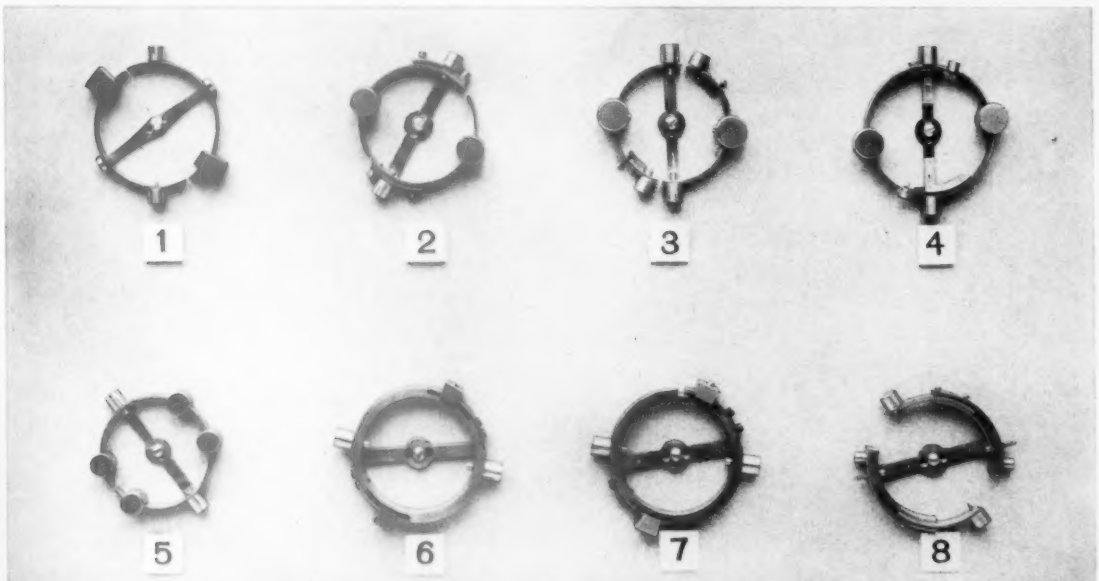


FIGURE 6 – *Types of compensation balance.* 1. *Modified Earnshaw type, having bimetallic arms. The positions of the small screws can be varied to vary the amount of compensation.* 2. *Poole's auxiliary compensation. Inward movement of the bimetallic arms with rise of temperature is unrestricted; outward movement with fall of temperature is somewhat restricted by the small screws on the short arms.* 3. *Kullberg's auxiliary compensation. Two small extra bimetallic arms are fitted, which can move inwards with rise of temperature but cannot move outwards with fall.* 4. *Mercer's auxiliary compensation. Similar in principle to Kullberg's.* 5. *Guillaume balance, which has four equal bimetallic arms, made of brass and a special nickel-steel, whose expansion coefficient is greater at low than high temperatures.* 6. *Uncut Invar balance with bimetallic affixes. The short bimetallic blades provide compensation for small residual temperature effects.* 7. *Uncut brass balance with bimetallic affixes. Similar to Guillaume's, but with heavier weights because greater compensation is required.* 8. *Balance with bimetallic affixes, for use with Elinvar balance spring. Compensation is varied by sliding the bimetallic affixes inwards or outwards. (From the set in the Science Museum, South Kensington. Reproduced by permission of Messrs. Thomas Mercer.)*

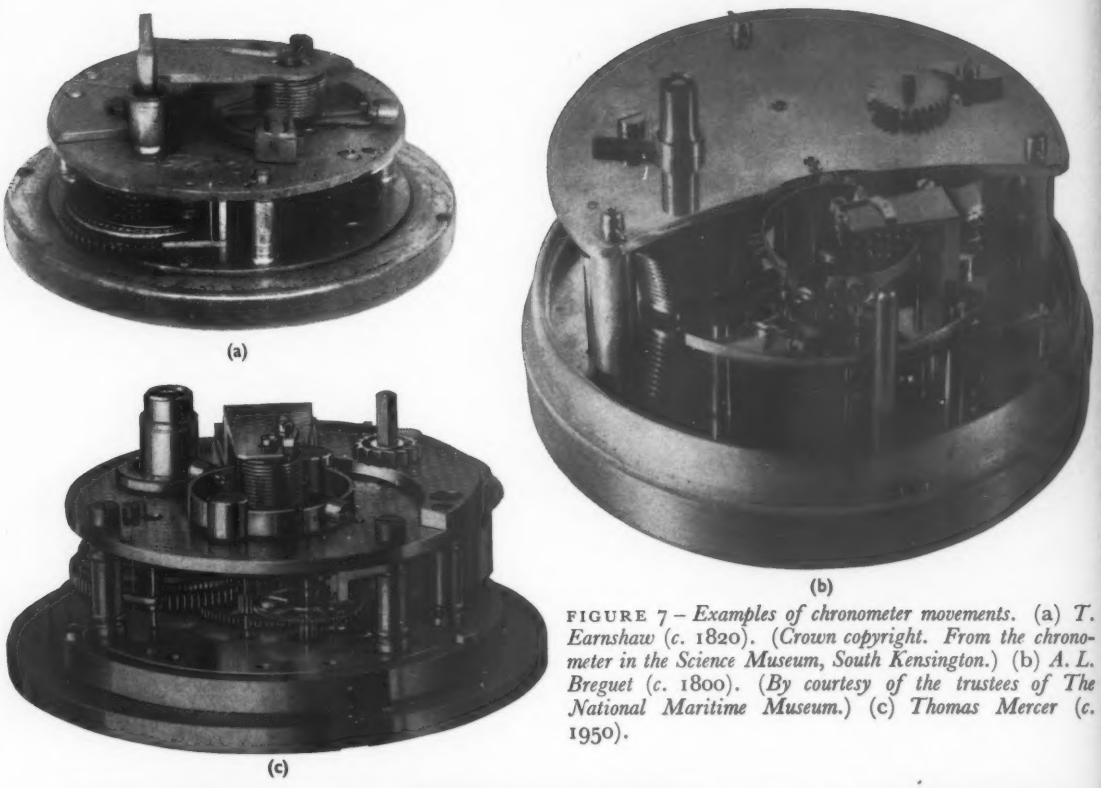


FIGURE 7 – *Examples of chronometer movements.* (a) *T. Earnshaw* (*c.* 1820). (*Crown copyright. From the chronometer in the Science Museum, South Kensington.*) (b) *A. L. Breguet* (*c.* 1800). (*By courtesy of the trustees of The National Maritime Museum.*) (c) *Thomas Mercer* (*c.* 1950).

FIGURE 8 – *Early and modern chronometers. Left to right: Thomas Mudge No.* 4 (*c.* 1790), *V. Kullberg* (*c.* 1916), *R. Pennington* (*c.* 1796), *and, in foreground, Thomas Mercer* (*c.* 1930) (*survey chronometer, with contacts*).

XI

timepiece and submitted it for trial. In many respects it was a remarkable and ingenious machine. It was controlled by two large balances, connected together by wires running over brass arcs so that their motions were always opposed, thereby counteracting the effects of a ship's motion. Four helical balance springs were used, and a gridiron arrangement was employed which, by slightly moving their inner ends, changed their tensions sufficiently to compensate for changes of temperature. The escapement was original in design and was practically frictionless. The machine, which weighed 72 pounds, was mounted in gimbals and tested on a voyage to Lisbon and back with encouraging results.

Harrison did not enter this timepiece for the full trial, but proceeded to construct a second, which was completed in 1739. In principle it was generally similar to the first, but with various improvements in detail. But it was not tested at sea, for in 1741 Harrison informed the Board that he was engaged upon a third machine which would surpass the first two. This machine was not completed, however, until 1757. The two balances, circular in form, were connected together by wires and controlled by a single flat spiral spring. Temperature compensation was provided by a device, termed a compensation curb, whereby the effective length of the spring was determined by two curb pins, whose position was controlled by a bimetallic strip.

On its completion, Harrison informed the Board that he proposed to apply for a trial at sea when he had completed a smaller timepiece, intended to be used with it as a deck-watch. This timepiece, completed in 1759, was a large pair-case watch, five inches in diameter. The large steel balance was controlled by a spiral steel spring, provided with a compensation curb, and its escapement was a much modified and improved type of verge. A most ingenious remontoire was provided, in which the spring was rewound every 7½ seconds, so that the driving force to the escapement remained practically constant.

Its timekeeping proved to be so good that Harrison decided to rest his claim for the award on its performance, and not to submit his large third timepiece for trial. In 1761 it was taken to Jamaica and back in H.M.S. *Deptford*, being tended by his son William. Its performance exceeded all expectations: the longitude of Jamaica was determined with an error of only 1¼′, or approximately 1½ miles. But though the requirements for the maximum award had been met, the Board felt that this accuracy might have been a fluke. A further trial was therefore arranged; the timepiece, again in charge of William Harrison, was placed on board H.M.S. *Tartar*, and the longitude of Jamaica was determined with an error of 9½′. On the return to Portsmouth it was found that in 156 days it had gained only 56 seconds.

But the Board was still not satisfied, on the ground that Harrison had not explained the principles of its construction. The final instalment of the award was paid only after Harrison had taken the timepiece to pieces before a committee nominated by the Board and after a duplicate had been made by another clockmaker. Larcum Kendall (1721–95) was chosen for this purpose, and completed the copy in 1770. This copy was taken by Captain Cook on his second and third great voyages in H.M.S. *Resolution*, and was paid glowing tribute by him. He remarked in his journal: 'Our longitudes can never be erroneous while we have so good a guide as Mr. Kendall's watch.'

Harrison's four timepieces and the Kendall copy of No. 4 are in the possession of the Royal Greenwich Observatory and are on loan to the National Maritime Museum at Greenwich, where they may be seen, all in going order.

The great achievement of Harrison was the proof that a timepiece could be constructed that was capable of keeping accurate time in a rolling and pitching ship. He realized the essential requirements for achieving this, but because of the complications of the design and the difficulties of construction none of Harrison's ingenious inventions has survived in the marine chronometer of today.

Thomas Mudge (1715–94), the inventor of the lever escapement now almost universally used in watches, became interested in marine timepieces after examining Harrison's No. 4. He made modifications to Harrison's design which were in the direction of over-elaboration instead of simplification; they included a constant-force escapement which, though perfect in theory, required an unusual degree of skill in construction. Mudge's workmanship was exquisite in its perfection, but was without influence on the subsequent development of marine timepieces.

The problem of designing a marine timepiece was meanwhile being tackled in France by Pierre Le Roy (1717–85) and Ferdinand Berthoud (1729–1807). Le Roy developed the first timepiece to embody two essential features of the

modern chronometer: the compensation balance and a 'detached' escapement, in which the balance is free from interference for almost the whole of its swing. He compensated for temperature changes by fitting two small thermometers to the staff of the balance, arranged so that with change of temperature the expansion or contraction of the mercury altered the moment of inertia by the amount needed to compensate for the change in the dimensions of the balance and the change in the strength of the balance spring. Le Roy completed his *montre marine* in 1766; it was tested at sea on a voyage to Newfoundland, when its performance was about equal to that of Harrison's No. 4.

Berthoud completed his first marine timepiece, which was a large, clumsy affair, in 1763. He was a man of extraordinary industry and of great originality. Trying one idea after another, and making successive improvements, he developed a timekeeper which in its essentials was not greatly different from the modern chronometer. He invented many different escapements, including several of the pivoted detent type and a spring detent escapement, of which he published a description in 1787. He made more than seventy marine timepieces in all.

So long as the making of a marine chronometer in its entirety remained the task of an individual highly skilled craftsman, the rate of production was necessarily slow and the cost was high. Two men in England, John Arnold (1736–99) and Thomas Earnshaw (1749–1829), converted the making of chronometers into a commercial proposition by simplifying the design as much as possible and employing workmen to do the subsidiary work and, after tuition, the more complicated and delicate parts also. They themselves undertook the final springing and adjusting, their methods being closely guarded as trade secrets. Each of them produced more than a thousand chronometers, at prices much below those of other makers.

Arnold made and patented several improvements in design. He devised several types of compensation balance and introduced the helical balance spring, now in general use. His first pivoted detent escapement was a somewhat clumsy affair, but he developed from it an efficient spring detent escapement which was used in all his subsequent chronometers.

To Earnshaw we owe the designs of the compensation balance and of the spring detent escapement (figure 9), which are essentially those in use today. Whether priority for the invention

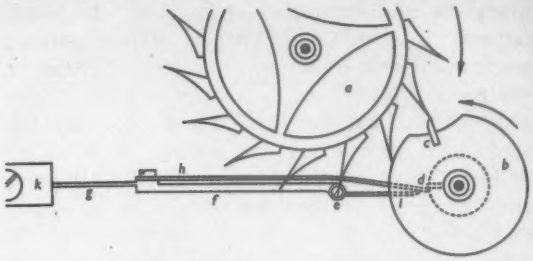


FIGURE 9 – *The spring-detent escapement. Key:* a, *escape wheel;* b, *impulse roller, attached to balance wheel;* c, *impulse pallet;* d, *unlocking pallet;* e, *locking pallet;* f, *detent;* g, *detent spring;* h, *passing spring;* i, *nose of detent;* k, *detent spring pad.*

of the spring detent escapement should be given to Berthoud, Arnold, or Earnshaw has been much discussed. They were probably working independently along similar lines, though perhaps each knowing something of what the others were doing. The spring detent was a natural development from the pivoted detent; it eliminated the irregularities caused by the thickening of the oil in the pivot. Earnshaw's design is the simplest in construction and the most efficient in operation. His original model, made by him for the Board of Longitude, is in the possession of the Royal Greenwich Observatory (figure 5).

The principle of this ingenious escapement may be seen from the figure. The detent, which carries the pallet for locking or 'detaining' the escape wheel, is attached to the detent spring, together with a light flexible spring made of gold, called the passing spring. The impulse roller, with the impulse and discharging pallets, is attached to the balance. In the position shown, the discharging pallet is about to trip the passing spring and to unlock the locking pallet, permitting the escape wheel to move forward. As it does so, the tooth adjacent to the impulse pallet gives an impulse to the pallet to maintain the oscillation of the balance. Meanwhile the detent spring has brought the locking pallet back to its original position, ready to lock the next tooth of the escape wheel. On the return swing of the balance the discharging pallet deflects the passing spring, which is so light that the effect on the balance is negligible. Thus the balance is almost completely detached, i.e. free from interference. An important feature of this escapement is that it requires no oiling.

Earnshaw brought the chronometer essentially to its modern design. Subsequent developments have been merely in matters of detail. It is surprising that in little more than half a century the

whole development from Harrison's timepiece, which won the £20,000 award, to the commercial development of the chronometer as we know it today, took place.

The principal modifications that have been made to chronometers since the time of Earnshaw may be summarized briefly. Arnold had found that the isochronism of the balance fitted with a helical spring depended on the shape of the terminal curve of the spring, and by trial he developed the shape of the curve that gave the best isochronism. In 1861 the French mathematician, Phillips, investigated the requirements for isochronism and showed that it is necessary for the centre of gravity of the spring to coincide with the axis of the balance. This condition is more easily satisfied with a helical spring than with a flat spiral spring, and the form of terminal used by Arnold complied closely with it.

Improvements have been made to the balance to provide better temperature compensation. With Earnshaw's design it is possible to adjust so that the chronometer has the same rate at two selected temperatures. Within this range of temperature the chronometer will gain slightly, and outside it will lose slightly. This effect is known as 'middle-temperature error'. Much ingenuity has been exercised to get rid of this error by the use of auxiliary compensations, of which there seem to have been as many different designs as makers of chronometers. The researches of Guillaume on the properties of nickel-steel alloys led him to the discovery of Invar, an alloy with a negligible coefficient of expansion, and of Elinvar, an alloy with a zero elasticity-temperature coefficient, which have found a useful application in chronometers. Elinvar balance springs were introduced by Ditisheim in 1920, while Hamilton employs an uncut balance of the invar type in conjunction with an elinvar spring. Careful control over the uniformity of the properties of these alloys is essential for their use in commercial manufacture, and they are best prepared in small quantities as a laboratory operation.

The design of the modern chronometer is such that uniformity of timekeeping to one or two tenths of a second a day over a wide range of temperature is attainable. For this precision great care in manufacture is essential; a high degree of finish, especially in the pivots, is needed; the materials must be carefully selected; the wheels of the movement must be accurately cut; and the oils used must be of suitable viscosities and have low viscosity-temperature coefficients.

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Book reviews

STATISTICAL ANALYSIS IN CHEMISTRY

Statistical Analysis in Chemistry and the Chemical Industry, *by C. A. Bennett and N. L. Franklin. Pp. xvi + 724. John Wiley and Sons Inc., New York; Chapman and Hall Limited, London.* 1954. 58*s. net.*

This is, on the whole, an attractively and lucidly written book, with many well chosen examples, and frequent reference to the underlying mathematical theory. Indeed, the amount of algebra seems at times unnecessarily formidable: there can be little advantage in proving at length, in an applied text, results that can perfectly well be accepted and understood by analogy with more fundamental formulae, detailed proofs of which are justifiably included. The chapter on the analysis of variance suffers particularly from this attempted comprehensiveness. This chapter shares two other faults with most texts on industrial statistics. All expected mean squares in analysis of variance tables are expressed in terms of variance components, even when this is admitted in the text to be inappropriate; and the dangerous practice, which may result in a biased variance, of pooling all non-significant effects with error is recommended and followed throughout. Many recently developed techniques are included, some valuable, others trivial refinements: more guidance on the relative importance of alternative methods would have been welcome. Despite these criticisms, this is an excellent survey of the field, and well worth the attention of any reader prepared to tolerate a certain amount of heavy, rather than advanced, mathematics.

M. R. SAMPFORD

PARADOXES

A Budget of Paradoxes, *by Augustus de Morgan* (with a new introduction by E. Nagel). *Pp.* 387. *Dover Publications Inc., New York.* 1954. $4.95 *cloth net.*

This very welcome reprint of a famous work by Augustus de Morgan is now issued in one volume. It is enriched with a short introduction by Professor Ernest Nagel of Columbia University, and it contains all matter, without omission, from the first and second editions. It is needless to recommend this delightful book to mathematicians. It most entertainingly discusses mathematical paradoxes in the manner of a commonplace book or bedside book. There is no method or order in the contents, but the errors of circle squarers are well to the fore. Mathematical paradoxers are among the camp-followers of science, but they

certainly should have their place in any comprehensive history of mathematics. Their errors, their prejudices, their ignorance, combined with their highly developed logical powers, would form a veritable series of case studies for the psychiatrist and the educationist. The reviewer cannot refrain from making two final comments. First, it is a tribute to the easy and unhurried life of professors in the spacious days of Queen Victoria that de Morgan had the time, energy, and opportunity to write so much about such apparently trivial matters. Secondly, it is very pleasant to recollect that many of these papers by de Morgan were originally published in the *Athenaeum*, a grave and serious periodical known to most of us only from the opprobrious comments made by Morris Finsbury in Stevenson's novel 'The Wrong Box.'

G. TEMPLE

LUMINESCENCE

Luminescence, with particular reference to inorganic phosphors. (*British Journal of Applied Physics, Supplement No.* 4). *Pp. iv* + 120. *The Institute of Physics, London.* 1955. 25*s. net.*

Twenty-one papers presented at a symposium held in 1954 are here collected into one volume. The main subjects treated are the development of new phosphors, chiefly for the lamp industry, electroluminescence, and the nature of luminescence centres. The approaches of the authors vary from the empirical to the highly mathematical, and the techniques from simple observations of fluorescence colour to detailed crystal structure analyses. The conclusions arrived at also vary strikingly; differences of opinion are expressed on the nature of the activators giving rise to particular bands, on the valency of activator ions and their crystal sites, on the size of the luminescence centres, on the question of association of centres, and other matters. In spite of the enormous strides made in the technical development of phosphors their behaviour and interpretation remain tantalizingly obscure. Although the most powerful techniques of crystal measurement have been applied, wave-mechanical calculations attempted, and new ideas such as charge-compensation and energy-transfer injected into the subject, the parts of the puzzle have not yet fallen into place, and still await some further touches of genius.

E. J. BOWEN

STATISTICAL MECHANICS

Elements of Statistical Mechanics, *by D. ter Haar. Pp. xix* + 468. *Rinehart and Company, Inc., New York.* 1954. $8.50 *net.*

In this book the author has carried out an ambitious programme—that of presenting the main results of statistical mechanics together with some of the applications. The space at his disposal has been used efficiently, and his clear style makes for a ready understanding. Details of mathematical manipulation might have been suppressed in some places, and the mathematical appendix replaced by references only. As a whole, however, the book covers a great deal of material, and it will be valuable to research students both as a textbook and as a reference work leading to some of the more recent applications.

There are four parts, the first dealing with independent particles, the second with ensemble theory, including ensembles in quantum statistics. The third part, the longest, deals with applications, and is the most exciting section of the book. A wide range of topics is covered, including condensation phenomena, electron theory of metals, semiconductors, cooperative phenomena, and rubber elasticity. There is a chapter on statistical methods in nuclear physics and a short account of theories of the origin of the chemical elements. The last part consists of a series of appendices on such subjects as the ergodic theorem, irreversible processes, the third law, and relativistic statistics. There is an extensive bibliography, up to about 1952.

Statistical mechanics is a branch of mathematical physics having an extremely wide range of applications, extending into astrophysics and chemistry as well as into the subjects mentioned above. The present book is a welcome addition to the existing literature on this dynamic subject.

L. S. GODDARD

SUPERFLUIDITY

Superfluids, Volume II (Macroscopic Theory of Superfluid Helium), *by the late F. London. Pp. xvi* + 217. *John Wiley and Sons Inc., New York; Chapman and Hall Limited, London.* 1954. 64*s. net.*

Superconductivity and the strikingly strange behaviour of liquid helium below the λ-point are among the most important subjects of low-temperature physics, and perhaps no other person did so much towards establishing a unified view of these two groups of phenomena as the late Professor Fritz London. The first volume of 'Superfluids', which dealt with superconductivity, appeared in 1950; this second volume, about liquid helium, was published posthumously, a few months after London's untimely death in March 1954.

The basic idea underlying this unified concept of the nature of superconductors and of liquid helium is that in these cases vanishing entropy near absolute zero is not connected with a positional order of the particles. Thus the atoms of liquid helium instead of being localized in space are, as it were, smeared out over a macroscopic region and order is brought about by a Bose-Einstein type of condensation in the momentum space. Frictionless flow in liquid helium and persistent currents in superconductors are manifestations of this ordering process with respect to momentum, and the fruitful two-fluid hypothesis is a direct outcome of these ideas.

London has written an indispensable and enjoyable book on this fascinating subject. Although this is essentially a theoretical study, experiments and their results are given their proper place and nowhere is mathematical formalism allowed to overshadow or to replace the physical meaning. It is perhaps unavoidable that in a book written round a central theme some aspects should be skimped, but the important thing is that the book brings out forcefully the now widely accepted view that the significance of superfluidity transcends the field of low-temperature physics. Indeed it seems that, as London pointed out in Volume I, the phenomena of superfluidity are pure quantum mechanisms, and 'although of macroscopic size, they are nevertheless withdrawn from the disorder of thermal agitation in essentially the same manner as is the electronic motion within atoms and molecules, in short, they are *quantum mechanisms of macroscopic scale.*'

The last word has not been said about liquid helium and superconductivity, and the theory may well take surprising turns. But London's contributions to the understanding of superfluidity is of such lasting value that, as Professor F. Bloch remarks in his foreword, any future work on this subject will still be permeated by London's spirit.

N. KURTI

ATOMIC PHYSICS

Introduction to Atomic and Nuclear Physics, *by Henry Semat. Pp.* 561.

Chapman and Hall Limited, London. 1954. 50*s. net.*

This is the third edition of Semat's 'Introduction to Atomic Physics,' revised and enlarged by the addition of nuclear physics. The book has grown out of a lecture course on modern physics, and can be recommended without reservation to student and teacher alike. The material is lucidly presented in a well worked out sequence, and carefully sub-divided into sections. A good balance is preserved throughout between logical and historical development. The text is attractively printed on good paper, and the illustrations are numerous and to the point. In particular there are excellent diagrams of apparatus and many good photographs. There are also numerous explanatory diagrams to illustrate more theoretical points (for example the scattering of α-particles by nuclei and the vector model of the atom), and the important formulae are boxed-in for emphasis.

The book is divided into three parts: foundations of atomic and nuclear physics; extranuclear structure of the atom; nuclear physics (including fundamental particles). The material is up-to-date to 1953, but sacrifices neither logic nor balance to topicality, and there are very few omissions. Such important recent developments as the detection of the neutrino, positronium, mesic atoms, and X-rays, and the new heavy mesons, are all described. Perhaps some of the references to early work underlying the most recent advances are a little haphazard, and the table of nuclear spins on p. 274 is very incomplete in comparison with other collections of data in the book. But these are minor criticisms when viewed against the general excellence of the book. M. H. L. PRYCE

THE SENSATION OF TONE

On the Sensations of Tone, *by Hermann L. F. Helmholtz (with a new introduction by Henry Margenau). Pp. xix* + 576. *Dover Publications Inc., New York.* 1954. $4.95 *net.*

Scientists will need no encouragement to read or re-read Helmholtz's celebrated work, which has by now an incontestable place as one of the great classics of natural philosophy. The present edition is a reprint of the last English edition of 1885 with a new, largely biographical, introduction by Professor Henry Margenau. But there can be few musicians or music-lovers who will not learn an astonishing amount from it.

For example: how many amateurs of 12-tone music realize how much of the public's aversion to it is based not on purely intellectual habit but on the physical prejudice of the ear, accustomed to a system of tonality developed over centuries? How many librettists, and particularly translators, realize to what extent the effect of a change of vowel sound on the quality of a particular note can be predetermined? And how many orchestrators realize the physical reasons for the different qualities of instrumental tone?

Musicians should read the interesting and controversial last chapter, in conjunction with the introduction, before starting on the whole work; they will then obtain a clearer picture of the outline and terms of reference which Helmholtz has chosen. Moreover, they will find that what at first appears to be a work of formidable length and somewhat unnerving complexity is in fact extremely lucid, and intelligible even to those without any previous knowledge of physics. MICHAEL BIRKETT

CHEMICAL DICTIONARY

Stewart's Scientific Dictionary (*fourth edition*), *by J. R. Stewart and F. E. Spicer. Pp.* 788. *Stewart Research Laboratory, Alexandria, Va; I. R. Maxwell and Company Limited, London.* 1953. 63*s.* 6*d. net.*

This dictionary of terms used in the chemical process industries now appears in its fourth edition since 1940. While this succession of editions should be an indication that the book is fulfilling a definite need, it does nevertheless seem at the moment to be in an unsatisfactory transitory state. It is now something more than a simple dictionary, but has not yet evolved into the encyclopaedia which is apparently the ultimate aim. There is much disparity between the entries, in their length, quality, and relevance; thus among the elements neither germanium, uranium, nor titanium—to mention but three metals which now have important and well known uses—have an entry. The titanium oxide pigments, by contrast, occupy two whole pages, and this preoccupation with products relating to paints appears in many other places. The entries relate largely to American practice and in consequence a number of important trade and technical terms used in Britain and other English-speaking countries are omitted—'Terylene' and 'Paludrine' are two examples. While the title of this book is misleading, it does nevertheless give some useful information on American chemical practice.

TREVOR I. WILLIAMS

MECHANISM OF CHEMICAL CHANGE

Atomic and Free Radical Reactions, *Volumes 1 and 2 (second edition), by E. W. R. Steacie. Pp. x* + 901. *Reinhold Publishing Corporation, New York; Chapman and Hall Limited, London.* 1954. £11 4*s. net.*

The extensive studies of the course of chemical change during the past decade have shown that many apparently complex reactions take place in a series of simple steps in which the active intermediates are atoms or radicals, and the present trend in chemical kinetics is towards obtaining quantitative information of the rate and activation energies of these elementary processes. This second edition of Dr Steacie's well known monograph is therefore particularly welcome, and in bringing his work up-to-date he has rendered a great service to all interested in the mechanism of chemical change. The growth of the subject, and the vast quantity of data which has appeared since the original publication in 1946, has necessitated a complete revision of the text and an expansion to nearly twice its original size. The work, which now appears in two fairly large volumes, provides a complete summary of the rates of all atomic and free radical reactions involving organic substances reported up to June 1953, and all work in the main journals up to September 1953. A brief introductory chapter on chemical kinetics is followed (chapters II–VI) by a general discussion of experimental methods, the determination of bond dissociation energies, and the role of atoms and radicals in thermal and photochemical reactions. The second volume (chapters VII–XV) gives a systematic survey of the data relating to the rates of the individual elementary reactions for systems containing carbon and hydrogen, oxygen, nitrogen, chlorine and fluorine, bromine, iodine, sodium, other metals, and sulphur. There is a bibliography of 2086 references and a reaction index. The amount of data in the book is immense and the author will earn the gratitude of many for his clear and critical presentation of each aspect of the subject. The book will remain the standard reference work on the subject,

but its high cost will compel the many research students and others who would treasure these volumes to use a library copy. C. E. H. BAWN

CHEMICAL PHARMACOLOGY

Introduction to Chemical Pharmacology, *by R. B. Barlow, with a foreword by H. R. Ing. Pp. xiv + 343. John Wiley and Sons Inc., New York; Methuen and Company Limited, London.* 1955. 35*s. net.*

A course of instruction for chemists is given in the Department of Pharmacology at Oxford by Dr H. R. Ing. The course is intended mainly for those who expect to enter the pharmaceutical industry, and covers the relation between structure and pharmacological action. It includes a practical class in methods of biological assay and of enzymology. Dr Barlow attended this course, and later worked for three years with Dr Ing; he has now written this book. It is an extremely courageous exposition of the structure-action relationship, and shows a grasp of the mechanisms of physiological action which is very surprising in a young chemist. It is well written and the presentation is interesting. After discussing the statistical treatment of biological results, the author deals with theories of narcotic action and then settles down to discuss the relationship between structure and action of analgesics like morphine, of drugs used in epilepsy, of stimulant drugs like strychnine, of local anaesthetics, of drugs like acetylcholine and nicotine, of atropine-like compounds, of curare-like compounds, of substances inhibiting cholinesterase, of adrenaline-like compounds, and of histamine-like compounds. The treatment is thorough, and well documented. The book will be of great value to many others as well as to those for whom it is specifically written, and the author is to be congratulated. J. H. BURN

INORGANIC CHEMISTRY

Les Gaz Inertes; l'Hydrogène—Les Halogènes, *by P. Laffitte and H. Brusset. Pp. 396. Masson et Cie., Paris.* 1955. *Paper covers, fcs 3600; bound, fcs 4200.*

In recent years inorganic chemistry has undergone a striking transition from an almost purely descriptive branch of science to a field in which all the modern developments of physics and chemistry find application. It is evident that any discussion of a chemical element or compound is complete only when the spectroscopic, structural, thermodynamic, and nuclear properties have been considered. Since the field of inorganic chemistry now embraces 101 elements a complete discussion of the whole subject is a formidable undertaking. The authors of the present volume have made a random selection of elements—the inert gases, hydrogen, and the halogens. In the discussion of these substances the authors have included enough of both the old and the new chemistry to bring out the most important features. They have not hesitated to deal with matters which may be considered outside the scope of inorganic chemistry and which are normally regarded as more appropriate to applied or organic chemistry.

The chapter concerned with the inert gases is a short one. It includes sections dealing with nuclear reactions involving α particles, the extraction of the inert gases from natural sources, the spectra of the inert gases, and the varied uses of the gases. The second chapter is devoted to the chemistry and physics of hydrogen. Sections are assigned to the structure and spectra of the hydrogen atom and the hydrogen molecule. An important discussion concerns the hydrides of the metals and the hydrogenation of various organic compounds. To complete this chapter an account is given of deuterium and its compounds, and of tritium. The final chapter is concerned with the halogens. A short account is given of element 85, the fifth halogen. The important advances in fluorine chemistry and in the chemistry of the inter-halogen compounds are given reasonable mention. This book is very readable and attractively produced. It cannot be said that it fills a long-felt want, for excellent books are now available on the subjects which the authors deal with, but it could find a useful place in most scientific libraries. W. WARDLAW

THE WIND

Man and the Winds, *by E. Aubert de la Rue, translated by Madge E. Thompson. Pp. 206. Hutchinson's Scientific and Technical Publications, London.* 1955. 18*s. net.*

It is only when gale warnings are broadcast on the radio or when we read of widespread damage done by winter storms that most of us pay any attention to the wind. In M. de la Rüe's book one reads, with some wonderment that it had not occurred to one before, how many and varied are the wind's influences. The author, who has travelled widely, keenly observing the winds in the many countries he has visited, gives a vivid account of their effect on health, the design and construction of dwellings, and on cultivation, as well as describing in detail the characteristics of most of the well known regional winds like the föhn, the chinook, the bora, and the mistral. There are chapters also on sailing ships, the wind in navigation and aviation, and the wind as a source of energy. The book is well written and illustrated and, with its many apt references, forms a useful contribution to the literature of climatology. It has been admirably translated, with many interesting notes supplementing the information given by the author, and has an adequate index. E. W. GOLDING

BIOLOGICAL EFFECTS OF RADIATION

Actions of Radiations on Living Cells (*second edition*), *by the late D. E. Lea. Pp. 416. Cambridge University Press, London.* 1955. 30*s. net.*

Lea's book, which first appeared in 1946, was immediately recognized as destined to be a classical contribution to radiation biology. The great theoretical interest of this field has always been apparent, and its practical importance, both for therapeutics and in connection with the utilization of atomic energy, is increasing continuously. It is most welcome that Lea's work, which has been out of print for some time, should now be made available again.

Lea did not attempt to review every aspect of the effects which radiations may produce on living systems. He approached the subject after a training in physics, and he concentrated his attention on those effects which seem most likely to depend on single ionizations, or small numbers of them, since these are the most susceptible to exact treatment and lead one to the fundamental processes which underlie the more complex phenomena. After a general discussion of the action of ionizing radiations on solutions, he therefore passes to such biological effects as the inactivation of viruses and the production of gene mutations and chromosome rearrangements. His treatment is in terms of the 'target' theory, and leans heavily (particularly in connection with gene mutations) on the earlier work of Timofeef-Ressovsky and his collaborators. More recent evidence, which suggests that the readiness with

which an ionization produces an effect is very dependent on the state of the biological system at the time of irradiation, has pointed to the necessity for considerable caution in adopting this hypothesis in its simple form. Nevertheless, Lea's treatment is an indispensable basis on which later work must build. In the new edition an appendix has been added giving some of the revisions and additions which he had made in his own copy of the book, before his untimely death soon after the first edition appeared. It can hardly be claimed, however, that the book is fully up-to-date; it is valuable rather as an exposition of principles than as a summary of present knowledge. C. H. WADDINGTON

LYSOGENIC BACTERIA

Les Bactéries Lysogènes et la Notion de Provirus, *by F. Jacob. Pp. viii* + 176. *Masson et Cie., Paris.* 1954. *Fcs* 800 *net.*

This monograph by Jacob is largely concerned with his studies on lysogeny in *Ps. pyocyanea*, and perhaps the most interesting contribution reported is the recognition of non-replicating agents from that species analogous to the colicines of *E. coli* strains. The main theme is, however, the behaviour of 'prophage' and the various ways in which induction (which results in the liberation of free infectious phage from the bacteria) can be provoked. There is no way by which prophage can be recognized in the lysogenic bacterium. It is not detectable serologically, and hence Jacob assumes that it is presumably in the form of nucleic acid incorporated into the genetic material of the bacterium.

This raises anew the old suggestion that phages are 'footloose' genes. In its new form the hypothesis assumes that a mutation occurring in the bacterial genome gives rise to an unstable locus which under appropriate stimulus is 'induced' to cause the production of a swarm of 'virus particles' and in the process lyse the host. Once virus particles have been produced in this fashion, they become susceptible to the interplay of mutation and survival and may evolve to the classic parasitic form of phage exemplified by T2. One may have the greatest sympathy with Jacob's view that lysogenic bacteria form the main reservoir of phages in nature without accepting this view of the phylogenesis of phages. The complete independence of immunological character and particularly the presence, in T2 at least, of a pyrimidine base not represented in bacterial deoxyribonucleic acid, suggests that we should have to go back very far indeed to find a 'common ancestor' of *E. coli* and phage T2, whether it was some proto-organism or a bacterial genome.

This, of course, is no reason whatever for not welcoming this lucid monograph on a fascinating topic which, perhaps more than any other biological theme, lends itself so freely to precise quantitative experimentation.

F. M. BURNET

BIOLOGY OF DESERTS

Biology of Deserts, *edited by J. L. Cloudsley-Thompson.* (*The proceedings of a symposium on the biology of hot and cold deserts organized by the Institute of Biology.*) *Pp.* 224. *Institute of Biology, London.* 1954. 14*s. net.*

The Institute of Biology organized a group of discussions on the biology of deserts and the present book is the outcome. It consists of about thirty contributions, and forms a remarkable group of papers, interesting, stimulating, and tending to produce a unified picture.

The term desert covers many types of environment, for deserts differ from one another in geology, soil, climate, vegetation, and fauna. We think that the book contains no definition of a desert: if that is so, it shows wisdom.

The great majority of contributions deal with some aspect of the great desert which stretches from the Atlantic in Morocco and Mauretania to Western India and Pakistan. But there are contributions also from workers in south-west Africa and the Australian deserts and to a rather slight extent from the American deserts. The cold deserts, that is to say the Arctic and Sub-Arctic, though included in the terms of reference, receive little attention.

It is a matter of considerable interest to see the extent to which the applied biologist is studying the less severe deserts, or even putting experiments into effect in the field. One of the early contributors points out that nomads are an extremely specialized type of human being, that if they are allowed to desert their camels and become lorry drivers or labourers in oil-fields, it would probably prove impossible to resurrect the nomadic way of life. The interesting suggestion is made that these nomadic graziers could become producers of meat for the outside world, if they could be guided by radar to places where rain has recently fallen; if the land could be preserved from over-grazing; and if particular types of forage could be encouraged. The applied botanists are giving much attention to the increase of desert shrubs as grazing, for either sheep or camels, some of these plants being leguminous and others saltworts.

P. A. BUXTON

BIOLOGICAL RECORDING METHODS

Einführung in die biologische Registriertechnik, *by Herbert Klensch. Pp. x* + 222. *Georg Thieme Verlag, Stuttgart.* 1954. *DM.* 33 *net.*

The author states that he has attempted in this book to give a simple introduction to the biological recording methods now generally in use. It is not clear what class of reader the book is intended for. The descriptions of the more elaborate methods, which are essentially research tools, are beyond the needs of the elementary student. But as a guide to research workers it apparently assumes that they have no knowledge of elementary physics, and have had no practical training in their degree courses; one must hope that such people are rare. The author's advocacy of simple methods, provided they are adequate, rather than elaborate, though more modern, methods, is to be commended. But in almost every section, the choice of the more elaborate methods to be described must be regarded as so incomplete as to detract seriously from the value of the book. For example, the section dealing with the measurement of the rate of fluid flow includes a description of Rein's *Thermostromuhr*, but no reference to the electromagnetic method introduced by Kolin and by Wetterer; nor, indeed, is there any mention anywhere of the bubble flowmeter or the Rotameter. Some of the very elementary material, on the other hand, might be condensed, and some platitudes omitted from the general introductory remarks; these, however, also contain some sound advice.

The book will be of value to British and American readers for its description of certain methods not commonly known to them, and for its references to European literature published in German. One is apt to neglect literature which is written in an unfamiliar language; it is unfortunate, however, that this book also suffers from the

same trouble, there being very few references to British or American literature among the total of 421 entries in the bibliography. L. E. BAYLISS

AMINOSUGARS

Biochemistry of the Aminosugars, *by P. W. Kent and M. W. Whitehouse. Pp.* 311. *Academic Press Inc., New York; Butterworths Scientific Publications, London.* 1955. 40*s. net.*

This book represents the first attempt to bring together our knowledge of the chemistry and biological functions of these substances since the publication of Levene's monograph in 1925. The intervening years have seen far-reaching advances, and a general survey of the subject was clearly overdue.

One part of the book describes the chemical properties of the aminosugars and gives a straightforward, though critical, account of the methods for their detection, estimation, and isolation. Biochemists who encounter aminosugars in the laboratory should find these pages of much practical value.

The other part deals largely with the complex mucosubstances which contain aminosugars, ranging from those of cartilaginous tissue and the gastrointestinal tract to the gonadotropic hormones and the newly discovered receptors for the influenza virus. The purification of these substances is very difficult. The authors rightly point out that few of the products obtained so far are likely to be single molecular species and that the relationship of such products to the complexes present in living organisms is uncertain; it may be, however, that they overestimate the extent to which the state of flux in biological systems will hinder chemical progress.

The functions of mucosubstances, long ago classed as supports, protective agents, and lubricants, are discussed in the light of recent discoveries, and the growing importance of enzymic studies is well presented. In this field much is obscure, and a full assessment of the situation could be given only in a larger book. However, the present volume, which contains many references, is undoubtedly a welcome addition to biochemical literature.

E. P. ABRAHAM

FORMATION OF NATURAL PRODUCTS

The Structural Relations of Natural Products, *by R. Robinson. Pp. xi* + 150. *Oxford University Press, London.* 1955. 25*s. net.*

The first Weizmann Memorial Lectures, delivered at Rehovoth in 1953, are collected in this book. During the last forty years Sir Robert Robinson has often suggested how a complex organic substance might be built up in plants and animals. The principles of chemical reactivity determining the choice of a laboratory method are not, it is assumed, greatly different for the living cell; although the cell uses enzymes, these are more likely to catalyse facile reactions than difficult ones. Thus by considering the initial materials available to the cell, a complex molecule may be analysed structurally and possible pathways of biosynthesis outlined. The possibility of deciding between one pathway and another hardly existed until recently; the use of isotopically labelled molecules and of genetically deficient mutants now ensures increasing knowledge of biochemical processes. On the whole, the above assumption stands confirmed: most biosynthetic reactions have their laboratory counterparts.

To anyone interested in biosynthesis, this book is a treasure-chest of ideas. Perhaps some will prove incorrect in detail: none can fail to stimulate. To give a known example, the lecturer suggested twenty years ago how the four-ring structure of cholesterol might arise by multiple folding of the linear molecule of squalene. The suggestion certainly stimulated K. Bloch in his experiments proving that squalene is indeed a precursor of cholesterol, although the precise manner of folding is not that originally put forward.

The first lecture deals with several chemical types, including terpenes, steroids, carbohydrates, and flavones. The second and third lectures are devoted to alkaloids. Structural analysis suggests, with high probability, that most alkaloids originate from amino-acids or their immediate precursors; indeed, the structure of some alkaloids has been correctly predicted by assuming such an origin. With this clue the lecturer guides his audience unerringly through a maze of the most bizarre-looking structures.

The large number of pictorial formulae probably explains the high price of the book, which is produced with an excellence characteristic of the Clarendon Press. J. W. CORNFORTH

PTERIDINES

Chemistry and Biology of Pteridines (A Ciba Foundation Symposium), *edited by G. E. W. Wolstenholme and Margaret P. Cameron. Pp. xiv* + 425. *J. and A. Churchill Limited, London.* 1954. 42*s. net.*

The Ciba Foundation generously supports a practice of calling together the chief active workers in various developing fields of research, and the proceedings of these meetings are published in book form. One of the meetings in 1954 discussed 'The Chemistry and Biology of Pteridines.' The interplay between the chemical and the biological aspects was continually stressed, so that this book makes invigorating reading for workers of a wide range of interests. The chemical section contains eleven papers which not only report original chemical investigations but which also collect together stores of information on such topics as ring-opening reactions and ultra-violet spectra. In addition there are several papers devoted to the constitution of various naturally occurring pteridines. The reports of the discussions which followed bear testimony both to the interest aroused by the speakers and to the skill of the chairman, Professor Adrien Albert.

The biological sessions included several papers on antimetabolites to the naturally occurring pteridines and their mode of action, as well as some clinical studies of disordered folic acid metabolism. Further studies of the role of the citrovorum factor in cell division were among the contributions made by Dr. W. Jacobson, who was in the chair for the biological sessions.

D. H. MARRIAN

MOSSES AND LIVERWORTS

British Mosses and Liverworts, *by E. V. Watson. Pp. xvi* + 419. *Cambridge University Press, London.* 1955. 45*s. net.*

This work describes about one quarter of the British species of mosses and about one sixth of the British liverworts, being those which occur more commonly. To one who had to learn his Bryophyta from the comprehensive works of Dixon and MacVicar, the boon to the student of a handbook that is not burdened with a plethora of rarities is obvious, although the beginner is apt to fear he may have mistaken a rarer, omitted relative for the commoner species. The drawbacks inherent in any such partial treatment have been greatly minimized by the inclusion in the keys of a considerable proportion of those that occur less commonly.

Only the test of field use by those without experience can yield a final judgment, but the author would appear to have provided a most useful handbook to initiate the novice in identifying members of these groups. Moreover, the ecological notes which he furnishes suggest the fascinating problems that the biology of these plants presents.

The text is illustrated with some two hundred informative line drawings and eighteen half-tone plates. One cannot but regret that the price may well place this work beyond the means of many of those to whom it might be most useful. E. J. SALISBURY

PLANT PHYSIOLOGY

An Introduction to Plant Physiology (*fifth edition*), *by W. O. James. Pp. viii + 303. Oxford University Press, London.* 1955. *17s. 6d. net.*

It is pleasant to welcome a fifth edition of James's 'Introduction to Plant Physiology.' Since it was first published in 1931 it has been a most useful textbook and one which has contrived to be modern as well as elementary. It has always been noted for lucid expression, clear illustrations, and for the large number of simple and informative experiments described. The new edition has been enlarged by 34 pages and 8 illustrations: it has been extensively re-written and reset. The physical properties of colloids and related matters have been brought together in a new chapter.

The author combines surveys of the range of behaviour—so interesting in biological material—with accounts of fundamental processes. Thus he gives tables showing the range of respiratory activity and of the respiratory quotient, and lists of the varied reactions of the plant to light and gravity. He also deals with the stepwise degradation of carbohydrate and with the organic acid cycle. How far should such topics enter elementary work? The intelligent pupil should be stimulated by such accounts: the less intelligent majority unfortunately tend to reproduce them from memory in examination papers, to the neglect of simpler and more easily understood matters. Perhaps the stimulation of the intelligent is more important. But this is an example of a continuing problem in the teaching of science to which no clear answer is apparent.

It is heartening to find the present position of such interesting topics as the first products of photosynthesis, the phototropic reaction, and flowering hormones simply and clearly stated. Dr James continues to earn the gratitude of pupil and teacher alike. M. SKENE

VERTEBRATE ZOOLOGY

Traité de Zoologie. Anatomie, Systématique, Biologie. *Vol. XII, Vertébrés, edited by Pierre-P. Grassé. Pp.* 1145. *Masson et Cie, Paris.* 1954. *Paper covers, fcs* 9800*; bound, fcs* 10 550.

In many ways, this thirteenth volume of the great *Traité de Zoologie* edited by Professor Pierre-Paul Grassé is the most important which has yet appeared, for it deals with general questions of morphology and embryology of vertebrates. The main lines of morphogenesis, gastrulation, head-segmentation, the architecture of the central and peripheral nervous systems, the paired sense-organs, the structure of the skull, axial and appendicular skeleton, teeth, vascular and urogenital systems, are all included. There are also chapters on the chromosomes of vertebrates, and on some of the biochemical characters (sterols, phosphagens, bile-salts, haemoglobin, percentages of various cations) of many groups of animals.

There is always a danger, in large and comprehensive works of this kind, that the natural desire to effect a broad synthesis may abrade and round off some of the irregular and apparently non-conformist results of detailed and objective analysis, obtained from observation and experiments on the diversified material. This danger has been completely avoided, in Professor Grassé's textbook, by the careful selection of his collaborators and the directives on which they have worked.

The various sections are succinctly written, up-to-date, and preserve a critical attitude to controversial problems, such as for example coefficients of cephalization or the nature of the trabeculae cranii. Beautifully produced and lavishly illustrated, this work is in every way worthy of the highest traditions of French zoology.

GAVIN DE BEER

HUMAN ANATOMY

Lehrbuch und Atlas der Anatomie des Menschen (*nineteenth edition*), *by F. Kopsch. Volume* 1, *pp.* 736*; volume* 2, *pp.* 768. *Georg Thieme Verlag, Stuttgart.* 1955. *DM* 64.50 *per volume.*

Rauber's textbook of Anatomy has passed through a long history, and though the appearance of its nineteenth edition is by no means a record for anatomical textbooks (in Britain, Gray's 'Anatomy' has reached its 31st edition), it is surely remarkable that Dr Kopsch himself has been engaged in the production of successive editions for over fifty years. German atlases of anatomy have always had a wide appeal (for example, the well known atlases of Spalteholz and Sobotta), mainly, no doubt, because the elaborate and carefully executed illustrations are so attractively reproduced. One is sometimes tempted to wonder how it is that German anatomists have at their disposal such highly skilled anatomical artists. Can it be because the publishers, having a comparatively large continental market at their disposal, are able to afford a high rate of remuneration? Possibly so, but apart from the technical efficiency of the illustrations the latter are often characterized by an accuracy of detail and a certain originality of presentation which convey an impression of the most intimate collaboration between the anatomist and his artist. The Rauber-Kopsch volumes, however, are more than an atlas, they combine an atlas and a textbook in the same production. In fact, of course, this is what all textbooks of human anatomy do, the only difference being that the illustrations are usually not so elaborately reproduced. Cunningham's 'Anatomy', for example, includes over 1200 illustrations, but since this standard book is not printed on thick art paper they have a somewhat less imposing appearance.

The question arises—do the illustrations really need to be so highly finished and so impressive as those in the volumes under review? One disadvantage is immediately obvious—the thick art paper adds enormously to the weight of the book. The current edition of Cunningham's 'Anatomy', we find, weighs nearly six pounds, while the two volumes of the Rauber-Kopsch work (which together contain about 150 fewer pages) weigh nearly eleven pounds. It can hardly be denied, also, that there is a certain misleading element in anatomical illustrations which are made to appear too realistic, for they may give the unsophisticated reader an impression of finality which is really not justified. All anatomical illustrations are, in a sense, diagrammatic representations, and the more elaborate and perfectly finished, the more likely they are to be accepted as something more than diagrams. For

example, neurofibrillae do not really exist in the form in which they are illustrated in these volumes, nor do the terminal reticula of nerve fibres, nor do the smaller lymphatic vessels. But these disadvantages are, of course, inherent in all anatomical illustrations which attempt an aesthetic combination of accuracy with clarity, and thus to present to the student the essence of his subject in an attractive and easily assimilable form. The illustrations in the Rauber-Kopsch atlas are, from this point of view, about as excellent as they could be. The text, also, is sound as a presentation in traditional style of purely descriptive anatomy. The section on the central nervous system is perhaps the least satisfactory, for it does not incorporate some of the more recent work on fibre connections (and from this point of view is somewhat outdated), and it also includes diagrams of fibre connections which almost certainly do not exist. As a textbook for students, the work is perhaps unnecessarily long and detailed, and for most students, of course, too expensive. But as a reference book in libraries it certainly has an important place.

W. LE GROS CLARK

NUCLEAR ENGINEERING

Introduction to Nuclear Engineering, *by Raymond L. Murray. Pp. xiv* + 418. *George Allen and Unwin Limited, London.* 1955. 30*s. net.*

Engineering students will increasingly concern themselves with the nuclear energy field, and many will have to become acquainted with a new and rapidly developing technology and with the basic science which lies beneath it. Professor Murray's book is intended mainly for readers in this category; they are assumed to have experience, at undergraduate level, of physics, mathematics, and chemistry.

The introductory chapters, on the fundamentals of atomic and nuclear physics, have wisely been made short; good texts are now available at introductory and more advanced levels, and useful lists of references for further reading are given throughout the book. These early chapters quickly converge upon discussion of the properties and reactions of neutrons, in the velocity range appropriate to nuclear energy work, and upon nuclear fission.

The scope of the remainder, amounting to some five-sixths of the total matter, is satisfactorily broad. There is naturally an extensive treatment of nuclear reactors, but in addition there are chapters on isotope separation, radiation hazards, shielding, disposal of radioactive waste, detectors and control instruments, neutron experiments, uses of radioactive and stable isotopes, nuclear propulsion, and electrical power production by nuclear energy.

In the chapters dealing specifically with nuclear reactors, the main types are contrasted and individually described, with illustration by reference to unclassified details of existing installations and with adequate presentation of the simple theory of the processes involved. The materials of reactor construction and the heat-transfer and fluid-flow problems of reactor cooling are discussed. There are two appendices, one on reactor theory and the other a table of nuclear data. Chemical engineering aspects, such as the processing of fuel elements, are outside the scope of this book and are referred to rather little, except for a brief discussion in connection with the disposal of radioactive waste.

Security classification now covers such small and detailed areas of the subject, outside the purely military sphere, that it has interfered very little with the author's purpose. The book should suit its intended readers very well. It is clearly written, and well illustrated with diagrams and with quantitative examples. Professor Murray rightly believes that his readers should be given an overall view of the main field, even though, in the nature of things, most of them will eventually specialize rather narrowly in their daily work.

T. G. PICKAVANCE

AMERICAN MEN OF SCIENCE

American Men of Science (*ninth edition*), Volume I (Physical Sciences). *Pp.* 2180. *The Science Press, Lancaster, Pa; R. R. Bowker Company, New York.* 1955. $20.00 *net.*

The extraordinarily rapid growth of the scientific profession in the United States is emphasized by the fact that in its new edition 'American Men of Science' appears in three volumes, instead of one as previously. The number of biographies has been increased from fifty thousand, in 1949, to ninety thousand. The volume which has just appeared relates to the physical sciences only, and contains some forty-three thousand entries; the two volumes to follow will deal with the biological and the social sciences respectively.

To review a reference work of this kind in the ordinary way is impossible, but sampling of the entries indicates that, as would be expected in a cumulative work of this kind, there are no notable omissions and that in each entry a commendable amount of information is given within a short space.

The tradition of using no more than one mark of punctuation at any point makes for brevity, the first essential in a work of this kind, but perhaps not always for clarity. This is, however, only a minor criticism of a most valuable reference book. One cannot but wish that other countries would compile similar directories with comparable thoroughness.

TREVOR I. WILLIAMS

Some books received

(*Note.* Mention of a book on this page does not preclude subsequent review.)

ASTRONOMY

Frontiers of Astronomy, *by Fred Hoyle. Pp. xvi* + 360. *William Heinemann Limited, London.* 1955. 25*s. net.*

Principes Fondamentaux de Classification Stellaire. *Pp.* 190. *Centre National de la Recherche Scientifique, Paris.* 1955. *Fcs* 1200 *net.*

Radio Astronomy, *by J. W. Pawsey and R. N. Bracewell. Pp. x* + 361. *Clarendon Press, Oxford.* 1955. 55*s. net.*

BIOLOGY

Animal Nutrition, *by E. J. Sheehy. Pp. viii* + 732. *St. Martin's Press, New York; Macmillan and Company Limited, London.* 1955. 30*s. net.*

Applied Entomology (*fifth edition*), *by H. T. Fernald and H. H. Shepard. Pp. ix* + 385. *McGraw-Hill Book Company Inc., New York.* 1955. $7 *net.*

Aux Confins de la Vie. Perspectives sur la Biologie des Virus, *by P. Morand. Pp.* 171. *Masson et Cie., Paris.* 1955. *Fcs* 850 *net.*

Bird Navigation, *by G. V. T. Matthews. Pp. vi + 141. Cambridge University Press, London.* 1955. 12*s.* 6*d. net.*

Letalfaktoren, *by E. Hadorn. Pp.* 338. *Georg Thieme Verlag, Stuttgart.* 1955. *D.M.* 39 *net.*

The Life of Bacteria, *by K. V. Thimann. Pp. xviii + 775. The Macmillan Company, New York.* 1955. $12.50 *net.*

Logique et dynamique du peuplement végétal, *by M. Guinochet. Pp.* 144. *Masson et Cie., Paris.* 1955. *Fcs* 880.

The Natural History of Tsetse Flies, *by P. A. Buxton. Pp. xx + 816. H. K. Lewis and Company Limited, London.* 1955. 84*s. net.*

Primates, *edited by W. C. Osman Hill.* Part 1: Strepsirhini, *pp. xxiii + 798.* Part 2: Haplorhini, *pp. xx + 347. University Press, Edinburgh. Part* 1, 1953, £5 5*s. net. Part* 2, 1955, 63*s. net.*

Some Physiological Aspects and Consequences of Parasitism, *edited by W. A. Cole. Pp. xi + 90. Rutgers University Press, New Jersey.* 1955. $2 *net.*

La Vie des Plantes, *by A. Guillaumin, F. Moreau, and C. Moreau. Pp.* 464. *Librairie Larousse, Paris.* 1954. *Fcs* 5190 *net.*

CHEMISTRY

Analytical Chemistry. The Working Tools, *edited by C. R. N. Strouts, J. H. Gilfillan, and H. N. Wilson. In two volumes, pp. xxi + 494 and ix + 496–1067. Clarendon Press, Oxford.* 1955. £5 5*s. net per volume.*

Chemistry of the Soil, *edited by Firman E. Bear. Pp. x + 373. Reinhold Publishing Corporation, London.* 1955. 70*s. net.*

Ionography, *by H. J. McDonald. Pp. x + 268. The Year Book Publishers Inc., Chicago.* 1955. 48*s. net.*

New Methods in Analytical Chemistry, *by R. Belcher and C. L. Wilson. Pp. xii + 286. Chapman and Hall Limited, London.* 1955. 30*s. net.*

Organic Reagents for Metals, Volume 1 (*fifth edition*), *edited by W. C. Johnson. Pp. viii + 199. Hopkin and Williams Limited, Chadwell Heath, Essex.* 1955. 15*s. net.*

Organic Syntheses. Collective Volume III, *edited by E. C. Horning. Pp. x + 890. John Wiley and Sons Inc., New York; Chapman and Hall Limited, London.* 1955. 120*s. net.*

Outlines of Enzyme Chemistry, *by J. B. Neilands and P. K. Stumpf. Pp. x + 315. John Wiley and Sons Inc., New York; Chapman and Hall Limited, London.* 1955. 52*s. net.*

Papírová Chromatografie, *edited by I. M. Hais and K. Macek. Pp.* 724. *Nakladatelství Československé Akademie Věd, Prague.* 1954. *Kčs* 142 *net.*

Solvent Properties of Amphiphilic Compounds, *by P. A. Winsor. Pp. ix + 207. Butterworths Scientific Publications, London.* 1954. 40*s. net.*

GENERAL

Better Ways. Nineteen paths to higher productivity. *Pp. ix + 97. British Productivity Council, London.* 1955. 2*s.* 6*d. net.*

Cells and Societies, *by J. T. Bonner. Pp.* 234. *Princeton University Press, Princeton, New Jersey; Geoffrey Cumberlege, London.* 1955. 25*s. net.*

If You Must Write——, *by W. H. Johnson. Pp. vi + 98. Hutchinson, London.* 1955. 4*s. net.*

Life, the Great Adventure, *by J. Rostand. Pp.* 258. *Hutchinson's Scientific and Technical Publications, London.* 1955. 12*s.* 6*d. net.*

Patent Law in the Research Laboratory, *by J. K. Wise. Pp.* 145. *Reinhold Publishing Corporation, New York; Chapman and Hall Limited, London.* 1955. 24*s. net.*

Precast Concrete, *by Kurt Billig. Pp. xvi + 341. Macmillan and Company Limited, London.* 1955. 32*s. net.*

Smoking and its Effects, *by S. Russ. Pp.* 144. *Hutchinson's Scientific and Technical Publications, London.* 1955. 8*s.* 6*d. net.*

GEOLOGY

Les Fossiles, *by E. Basse de Ménorvae. Pp.* 124. *Presses Universitaires de France, Paris.* 1955. *Fcs* 153.

Nuclear Geology (A Symposium on Nuclear Phenomena in the Earth Sciences), *edited by H. Faul. Pp. xi + 414. John Wiley and Sons Inc., New York; Chapman and Hall Limited, London.* 1955. 56*s. net.*

HISTORY OF SCIENCE

The Botany of Cook's Voyages, *by E. D. Merrill. Pp. iv + 161–384. Chronica Botanica Company, Waltham; William Dawson and Sons Limited, London.* 1954. $4.75 *net.*

Causalités et accidents de la découverte scientifique, *by R. Taton. Pp.* 172. *Masson et Cie., Paris.* 1955. *Fcs* 980.

Discoveries and Inventions of the Twentieth Century, *by J. G. Crowther. Pp. xvii + 432. Routledge and Kegan Paul Limited, London.* 1955. 30*s. net.*

MATHEMATICS

From Simple Numbers to the Calculus, *by Egmont Colerus. Pp. xi + 255. William Heinemann Limited, London.* 1955. 25*s. net.*

MEDICINE

Erreger und Überträger tropischer Krankheiten, *by R. Geigy and A. Herbig. Pp. xxiv + 472. Verlag für Recht und Gesellschaft AG., Basel.* 1955. *Swiss fcs* 80.

Le Poumon, *by A. Policard. Pp.* 264. *Masson et Cie., Paris.* 1955. *Fcs* 1500.

PHILOSOPHY

Thoughts About Life, *by F. Friedburg. Pp.* 40. *Philosophical Library, New York.* 1954. $2.50 *net.*

PHYSICS

Annual Review of Nuclear Science, Volume 4, *edited by James G. Beckerley. Pp. ix + 483. Annual Reviews Inc., Stanford, California.* 1954. $7 *net.*

Atomic Energy Research at Harwell, *by K. E. B. Jay. Pp. xii + 144. Butterworths Scientific Publications, London.* 1955. 5*s. net.*

Einführung in die Quantenelektrodynamik, *by W. Thirring. Pp. xii + 122. Franz Deuticke, Vienna.* 1955. *D.M.* 17.50 *net.*

A Guide Book to Electricity, *by J. H. M. Sykes. Pp.* 275. *Hutchinson's Scientific and Technical Publications, London.* 1955. 21*s. net.*

A Handbook of Hard Metals, *by W. Dawihl. Pp. viii + 162. Her Majesty's Stationery Office, for Department of Scientific and Industrial Research, London.* 1955. 25*s. net.*

The Laws of Nature, *by R. E. Peierls. Pp.* 284. *George Allen and Unwin Limited, London.* 1955. 21*s. net.*

Physics and Microphysics, *by Louis de Broglie. Pp.* 286. *Hutchinson's Scientific and Technical Publications, London.* 1955. 21*s. net.*

Quantum Theory of Solids, *by R. E. Peierls. Pp. viii + 226. Clarendon Press, Oxford.* 1955. 30*s. net.*

Notes on contributors

C. P. WHITTINGHAM,
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Was born in London in 1922 and was educated at Owen's School, London, and St. John's College, Cambridge. After taking a research degree at Cambridge he spent a year with Professor Emerson at the University of Illinois; last year he was a visiting professor at the University of Minnesota. His researches at Cambridge have been on the physiology of photosynthesis. In collaboration with Robin Hill he has recently written a monograph on photosynthesis, and he is the author of numerous papers on this subject.

ANN WYLIE,
M.Sc.,

Was born in Wellington, New Zealand, in 1922 and was educated at the University of Otago. She came to England in 1947 and worked under C. D. Darlington, at the John Innes Horticultural Institution, on the cytology and history of daffodils and roses. In 1952 she joined the staff of the Botany Department of the University of Manchester, where she is now a lecturer. She is now collaborating with C. D. Darlington in preparing the second edition of Darlington and Janaki-Ammal's 'Chromosome Atlas of Cultivated Plants'.

R. SNOW,
M.A., B.Sc., F.R.S.,

Was born in 1897 and educated at Winchester College and, after service with the Royal Artillery in the war of 1914–18, New College, Oxford. Has been a Fellow of Magdalen College, Oxford, since 1922. His botanical researches have been principally on the response of plants to stimuli, the correlation between their growing parts, and the determination and location of leaves. In this last field he has worked mainly in collaboration with his wife.

J. N. ALDINGTON
B.Sc., Ph.D., F.R.I.C., F.Inst.P., F.I.E.S., M.I.E.E.,

Was born in 1905 and was educated at the Balshaws Grammar School, Leyland, the Harris Institute, Preston, and the Technical College, Blackburn. He has been with Siemens Electric Lamps and Supplies Limited since 1923, and is managing director of that firm and of Alfred Graham and Company Limited. In August 1955 he was appointed managing director of Siemens Brothers and Company Limited. He is author of various papers and articles dealing particularly with developments in electric discharge lamps. He has twice been awarded the Leon Gaster Memorial Premium for theses on fluorescent light sources and their applications and on bright light sources; he has also been awarded the Crompton Premium of the Institution of Electrical Engineers. He is a member of the National Illumination Committee of Great Britain and of the British National Committee of the International Electrotechnical Commission.

H. W. CUMMING,
B.Sc., A.R.I.C.,

Was born in Preston in 1921 and educated at Preston Grammar School and the Harris Technical College. Since 1940 has been engaged in research in the laboratories of Siemens Electric Lamps and Supplies Limited, particularly upon electrical discharges in gases and vapours. In 1951 was awarded the Leon Gaster Premium of the Illuminating Engineering Society.

L. J. AUDUS,
M.A., Ph.D.,

Was born in 1911 and was educated at the University of Cambridge. Was on the botany staff of University College, Cardiff, from 1935 until the outbreak of the last war, when he took a commission in the R.A.F.V.R. and went to Singapore in command of a radar unit. Spent the last 3½ years of the war in Japanese prison camps in the South Pacific. On demobilization, joined an Agricultural Research Council Unit of Soil Metabolism to investigate problems of weedkillers in soils. His interests extended into the fields of soil microbiology and plant growth hormones, with which his present research is concerned. In 1948 was appointed to the Hildred Carlile Professorship of Botany at Bedford College, University of London. He is the author of one book, *Plant Growth Substances* (1953), and research articles on plant respiration and plant growth hormones, particularly in relation to roots.

SIR HAROLD SPENCER JONES,
K.B.E., M.A., Sc.D., D.Phil., Ll.D., F.R.S., F.R.S.E.,

Has held the position of Astronomer Royal since 1933. He was born in London in 1890 and was educated at Latymer Upper School, Hammersmith, and Jesus College, Cambridge. From 1923 to 1933 he held the post of His Majesty's Astronomer at the Cape of Good Hope. He was knighted in 1943. He has received the Royal Medal of the Royal Society, the Gold Medal of the Royal Astronomical Society, the Janssen Medal of the Astronomical Society of France, the Bruce Gold Medal of the Astronomical Society of the Pacific, and the Gold Medal of the British Horological Institute. He is an Honorary Fellow of Jesus College, Cambridge, a past president of the Royal Astronomical Society, of the British Astronomical Association, of the Institute of Navigation, of the International Astronomical Union, and of the Society for Visiting Scientists. He is president of the British Horological Institute. He is a foreign member of many national academies and an honorary member of many Dominion and foreign astronomical societies.

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